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THE ORIGIN AND PROPERTIES OF THE EUROPEAN BLACKBERRY FLORA

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POLYMORPHY.

THE genus *Rubus* being spread over all continents and occurring in all climatic regions is split up into several subgenera presenting the most diverse appearance. FOCKE, who studied the genus for more than fifty years, estimated in 1914 the number of species at approximately 400. Of these, 130 belong to the blackberries in the wide sense of the word (subgenus *Eubatus*). The North-American and especially the European blackberries have consistently worried the botanists, but now — owing to the unwearied taxonomical efforts of FOCKE, SUDRE, ROGERS, and others — we know the principal outlines of the European blackberry flora, its systematics and geography. LIDFORSS, the pioneer experimental taxonomist, who died in 1913, explained how the diversity and multitude of types once arose and how new biotypes may still arise. Most of his outstanding genetical experiments, the first of their kind, were unfortunately published only in Swedish. A short review of his results (1914) was brought posthumously to print in German by JOHANNSEN, but previously to this a brilliant essay on the taxonomy of polymorphous species and genera was already available to foreign scientists (1907 b).

The European blackberries are in nature divided into two great complexes: the *Moriferi* (*Eubati*) *veri* and the *Corylifolii*. The latter complex is morphologically and genetically related to the tetraploid Linnean species, *R. caesius*, which is widely distributed. In fact, it is proved by LIDFORSS's experiments that the Rubi Corylifolii are primary and secondary cross products of Moriferi veri and *R. caesius*. Such crosses, together with back-crosses and inter-crosses of Corylifolii, arise continuously over wide areas, rapidly changing the *Rubus* populations of the local floras. This can especially be noticed in regions where the Moriferi veri live on the outskirts of their possible distribution area and have become genetically stable. The number of biotypes in southern Scandinavia is certainly more limited than farther South but is still enormous. Twenty or thirty Scandinavian complexes are worthy of taxonomical description.

To give the reader an idea of the profusion and abundance of European blackberries, it may be mentioned that SUDRE in his monograph of 1908—1913 listed 109 main or circle species of Moriferi veri, around which were placed 691 more or less distinct species containing in all 1927 varieties given Latin names. In the index no fewer than 3350 different names, applied to species, varieties or supposed hybrids, were enumerated. Certainly several hundred other types were previously described and named.

Using SUDRE's classification of the European Moriferi veri, we find that *Rubi Suberecti* (I) comprise 7 circle and 19 minor species containing 40 named types, *Rubi Silvatici* (II) 41 circle and 160 minor species with 316 types, *Rubi Discolores* (III) 11 circle and 76 minor species with 244 types, and *Rubi Appendiculati* (IV), finally, 50 circle and 440 minor species with 1327 named types. Of special interest among the Appendiculati are *Rubi Glandulosi*, which have a rather south-eastern centre of distribution (Hungary, the Caucasus) but are also common in Austria, Switzerland and France. They comprise only nine circle species, but these are split up into 112 minor species with no fewer than 516 variations and contain the single representatives acclimatizing at high sea-levels in the Alps (GUSTAFSSON, 1933).

Most of the blackberries occupy a restricted area, but about one hundred types are distributed over great parts of the European countries. The astounding confusion of local and widely distributed types is simply due to the occurrence of pseudogamy, i. e. parthenogenetic embryo formation accompanied by sexual endosperm development, maintaining in nature heterozygous segregates and hybrid derivatives. Most of the widely distributed types consist of small, rather uniform populations which continually produce some rare aberrants by means of hybridization or segregation. Primary hybrids breed sexually. Sooner or later pseudogamous types appear in their progenies, combining genes and chromosomes in a new manner. Now and then some segregates enjoy an increased vitality and a potent capacity of propagation by seeds — in addition to the multiplication by rooting stem-tips — and spread widely.

THE OCCURRENCE OF PRIMARY SEXUALITY.

Inspecting the shape and appearance of the pollen FOCKE (1877, 1914) postulated the occurrence of some primary species, viz. *R. caesius, tomentosus, ulmifolius, incanescens* and *caucasicus*, to which accord-

ing to him *R. gratus* and *Arrhenii* could probably be added. *R. caesius* is, however, tetraploid over great parts of its distribution area, and studies of its pollen size have so far indicated no occurrence of diploid ancestors still alive. In experiments it propagates by ± complete apomixis. *R. tomentosus* is sexual and diploid, similarly *R. ulmifolius* (= *R. rusticanus* in CRANE and DARLINGTON, 1927, and in later English papers). *R. incanescens*, *R. Bollei* and *R. caucasicus* have a pollen-grain size and quality characteristic of diploid blackberries, indicating a primary sexuality. *R. Arrhenii* and *gratus* are both tetraploid and probably apomictic.

The European Rubi Suberecti are closely allied to North-American blackberries, especially to the species *R. villosus*, *allegheniensis* and *canadensis*, the first two of which are diploid (LONGLEY, 1924). *R. allegheniensis* is known to be sexual (PEITERSEN, 1921). Among the European Suberecti no sexuals have been found, and by chromosome counts and pollen analysis it was ascertained that every one examined had the tetraploid or triploid chromosome number. Since the morphological similarity is so pronounced, we may postulate, either that diploid Suberecti related to the North-American sexuals have once occurred in Europe and are now extinct, or that the European polyploids have arisen in some way or other in North-America and migrated from there. The latter interpretation is hardly plausible, as all examined North-American Moriferi veri are sexual (PEITERSEN). The west-American, »auto-apomictic» species *R. vitifolius* or *ursinus*, studied by CRANE and THOMAS (1940), belongs to another section.

From a taxonomical point of view crosses between the enumerated sexuals are sufficient to explain the polymorphy within Moriferi veri. The two opposite extremes consist of the proposed sexual of Rubi Suberecti and of *R. caucasicus* within Rubi Glandulosi. Rubi Silvatici, Discolores and part of the Appendiculati may morphologically be derived from *R. ulmifolius*, *incanescens* and *tomentosus* and their crosses with one another, with the postulated *R.* »*suberectus* f. *amphimicta*» (a sexual form) and with *R.* »*glandulosus* f. *amphimicta*» (*R. caucasicus*). This does not imply that other diploids have not taken part in the production of apomicts and polyploids. *R. Bollei* from the Canary Islands is an example of an African species presumably having a primary origin.

Thus we may conclude that if the European blackberries once arose from diploid sexuals, these should be relatives of a series of species more or less resembling the above-mentioned primary types. The few

discovered or postulated diploids suffice to account for the multitude of apomicts occurring. As early as 1914 this fact was pointed out by FOCKE and further stressed by the present writer in 1930 and 1939. The similarity to the results obtained in *Crepis* by BABCOCK and STEBBINS (1938) is obvious. In the latter genus, however, the apomicts do not only represent polyploid recombinations of the diploid species (allopolypoids) but they behave to a great extent as quantitative changes, originating by autopolyploidy. In *Crepis* great swarms of polyploid apomicts have grouped themselves closely around the diploid sexuals still alive.

DERIVED SEXUALITY.

Recent studies in *Poa pratensis*, *Poa alpina* (MÜNTZING, 1940; ÅKERBERG, 1939, 1942) and *Potentilla* (MÜNTZING, 1941, p. 259) have shown that the recessive behaviour of apomixis as illustrated by *Rubus* crosses (GUSTAFSSON, 1930) is a spread phenomenon. Most probably in all three genera apomixis reappears in late progenies of hybrids after a process of partial homozygotising (inbreeding). *Poa* and *Rubus* differ in certain features. Recombinations due to self-fertilization or to autosegregation (cf. p. 269) take place in *Rubus* without altering the apomictic mode of propagation. In fact, apomixis becomes even more stable in these instances (LIDFORSS, 1914, p. 12). [Cf. also the hybrid between two related *Potentilla Tabœrnemontani* biotypes (MÜNTZING, 1941, p. 266).] In *Poa* polyhaploids, polytriploids, normal crosses as well as segregations due to self-fertilization involve a disappearance of apomixis. The genera cannot, however, be exactly compared, as crosses and segregations in *Poa* alter the chromosome number, owing to the aberrants having lost or gained some chromosomes. Studies on autosegregated types — if such occur in *Poa* — will prove for certain whether changes in the genic constitution as well as in the chromosome balance shift the apomictic multiplication into sexual.

The recessive condition of apomixis in *Rubus* and *Poa* affords an enormous potential source of new variants. Most of the segregates no doubt disappear rapidly, but in the case of successful recombinations some will survive in nature. The behaviour of derived sexuals was analysed by LIDFORSS in several cases, one of which is especially striking.

In the summer of 1899 a presumed hybrid of *R. caesius* and *R. Wahlbergii* (the last-mentioned type belonging to Rubi Corylifolii)

was found in southern Sweden, resembling fairly closely a type named *R. acutus* by LINDEBERG. After controlled self-pollination (the pollen fertility was almost 100 %) a great number of seedlings were obtained. None of the full-grown F_2 plants agreed completely with the F_1 plant. Some were still 1) *acutus*-like (the prickles being unequal in length and shape) but differed in various respects. A gigas-form resembled somewhat the spontaneous type *R. hallandicus*. Another group consisted of 2) *pruinosus*-like types (*R. pruinosus* having 7-nate stem leaves and acicular prickles), one being a pronounced transgression as to earliness. 3) Two *permixtus*-like types were found, one of which showed constitutional disturbances (*R. permixtus* ARESCH. is a poorly known type from south-eastern Scania). 4) That certain segregates would resemble one of the proposed parents, *R. Wahlbergii*, could be expected (concerning *R. Wahlbergii*, cf. p. 255). 5) *R. acuminatus* LINDEB. = *R. gothicus* FRID. et GEL. is a well-defined complex within the Corylifolii. Two specimens, morphologically related to this type, appeared. Further, LIDFORSS supposed 6) that a segregate characterized by numerous glands, acicular prickles, very broad end-leaflets, etc., should be placed close to the German *R. polycarpus*. 7) Very interesting from a taxonomical point of view was the origin of a segregate very closely allied to the primary species *R. tomentosus*. 8) Other segregates were identical with the spontaneous *R. ruedensis* growing in nature not very far from the locality of the hybrid. 9) That the second proposed parent, *R. caesius*, which has produced the multitude of different Rubi Corylifolii, should reappear in a more or less deviating shape, is not surprising. 10) Some F_2 descendants, finally, had a very singular appearance, outpassing all variations known from nature.

This analysis, continued for two further generations, proves that the derived sexuality is a property of great importance for the origin of new biotypes. In fact, this property implies one of the two factors creating the equilibrium system in *Rubus* and *Poa*.

CHROMOSOME NUMBERS.

MORIFERI VERI.

Previously the present writer published a list of chromosome numbers in Scandinavian and other Moriferi veri (1939), and since then a great number of new counts have been made. A complete survey will be postponed to the detailed cytogenetic monograph under

preparation. Except for a small number of triploids and pentaploids, all apomicts occurring in nature are tetraploid, possibly with some monosomic or trisomic types arising infrequently. Unfortunately the number of Rubi Glandulosi examined is very small, owing to the fact that they are rare in Northern Europe. A collecting trip in 1929 to the boundary regions of France and Germany gave but few cytological results. So many different apomicts have been investigated, however, by the writer, by CRANE, DARLINGTON and THOMAS (1927, 1940) and by DATTA (1932) that we may safely conclude that the great mass of European Moriferi veri possess 28 somatic chromosomes. The chromosome number appears to be stabilized, not having been continually increased as in *Alchemilla*, *Crepis*, *Poa* and other genera. With the exception of one garden product of *R. Borreri*, examined at John Innes Horticultural Institution, the hexaploid number is not met with, either in gardens or in nature.

Some of the triploid and pentaploid complexes are of taxonomical interest. Especially noteworthy are *R. nitidus*, *thyrsoideus* (sp. coll.) and *R. Bellardii*, the first two being triploid.

R. nitidus WHE et N. is a widely spread type, growing in somewhat moist or even swampy soil, known from South-Sweden, the island of Bornholm, West and Northwest Germany, northern and western France down to Bordeaux, Great Britain, Austria, Switzerland. Possibly it also occurs in Portugal.

It differs from other Scandinavian blackberries by strongly curved prickles in the inflorescence, green, somewhat prickly sepals and a characteristic leaf-shape.

Some varieties and hybrids have been described, but it holds nevertheless an isolated position among the Suberecti. In 1885 ARESCHOUG described a variety of *R. nitidus* named *grandifolius*, originally regarded as a primary hybrid between *R. insularis* and *nitidus*. This interpretation was supported by LIDFORSS (1907 b).

The triploid chromosome number together with the morphological constancy in nature argues for the occurrence of pseudogamy. Cytologically it must be regarded as an autotriploid.

The old name *R. thyrsoideus* WIMM. is assigned to a collective group, including among other blackberries *R. thyrsanthus*, *candicans*, *elatior* and *phyllostachys*. The triploid chromosome status has been settled in four members of the complex, viz. *R. thyrsanthus*, its subtype *subvelutinus*, *R. candicans* and *R. elatior*.

R. thyrsanthus F. is distributed along the sea-shores of Sweden and Norway, is found in Denmark, occurs in Germany from the Vistula to North-Sleswick, eastern Harz and Thuringia, probably also in Bohemia and Moravia. According to FOCKE (1902), *R. thyrsanthus* includes a polymorphous series of types, the end-links of which are connected with *R. candicans*, *sulcatus* and *plicatus*. By means of dried specimens it cannot be accurately separated from *R. candicans*, *phyllostachys* and *pubescens* (?). Nevertheless this type is highly characteristic in Scandinavia, where the other members of the group are almost absent.

R. candicans WHE et N. resembles, except for the related Thyrsoidei, the vigorous forms of *R. tomentosus* and blackberry types as, for instance, *R. pubescens, sulcatus* and *Vestii* (FOCKE). It has a more western distribution than *R. thyrsanthus* but occurs also in Austria and Moravia. A great number of variations and supposed hybrids were described by SUDRE.

R. thyrsanthus is almost entirely pseudogamous (LIDFORSS). Only once was an artificial hybrid obtained.

R. thyrsanthus, candicans and *elatior* behave cytologically as autotriploids.

R. Bellardii WHE et N. (GUSTAFSSON, 1933) is distributed over great parts of Europe and appears to be very uniform in nature — »species constans» (FOCKE). Even SUDRE does not mention more than one unimportant variation and three presumed hybrids. In Sweden two endemic blackberries, *R. vestervicensis* and *R. aureolus* var. *subglandulosus*, have been regarded as hybrids of *R. Bellardii*.

Cytologically *R. Bellardii* cannot be denoted as a pronounced autopolyploid, but frequent multivalents occur. It occupies a position between auto- and allopolyploidy.

RUBI CORYLIFOLII.

No diploid Corylifolii are known and can hardly be expected to occur (unless as haplo-tetraploids), since the Corylifolii arise as crosses of the tetraploid *R. caesius* and various Moriferi veri. In Scandinavia no triploids have been found so far. In regions where the diploid species *R. tomentosus* and *ulmifolius* are common, related Corylifolii occur, frequently highly sterile. The sterility may be accounted for by a possibly occurring triploid chromosome number, by partial gone degeneration and the exclusive formation of reduced egg-cells.

The great mass of Corylifolii are either tetraploid, pentaploid or hexaploid, but the tetraploid number is plainly predominant, distinct complexes especially belonging to this category (*R. aureolus, ciliatus, centiformis, eluxatus, fioniae* with its subtype *benefixus, glaucoformis, gothicus, hallandicus* and *rosanthus* var. *lejocarpus*). *Acutus*-like and other unequal-prickled Corylifolii possess in many instances 42 chromosomes, this frequently being the case also with indistinct and locally restricted segregates and crosses. One well-defined hexaploid is *R. cyclophyllus,* occurring in western Sweden.

Of great interest are three pentaploid complexes, *R. Wahlbergii* ARRH., *R. pruinosus* ARRH. and *R. Lagerbergii* LINDEB. The first two are rather polymorphous in nature, but nevertheless they are easily distinguished from tetraploid and hexaploid types. The pentaploid number of *R. Wahlbergii* and *R. pruinosus* has been ascertained in many collections from different parts of Sweden, Denmark and Norway, also when the deviations in vigour and morphology were prominent.

In what manner these types originally arose, is of course shrouded in obscurity. LIDFORSS produced, however, a *Wahlbergii*-like F_1 by the cross *R. thyrsanthus* × *caesius*, and taxonomical data gathered by previous batologists as well as by the writer himself confirm such an interpretation for part of the spontaneous *R. Wahlbergii*. With reference to the auto- or allopolyploidy of these pentaploids, see p. 259.

Consequently Rubi Corylifolii have not become stabilized chromosomally to the same extent as Moriferi veri. Most of the distinct types are either tetraploid or pentaploid, however. Rubi Corylifolii are more or less anthropochorous in their distribution, more so than Moriferi veri, and edaphically acclimatized to road-sides, ditches, and so on. Generally their fruit-setting is more or less decreased. They rarely spread over large areas but form ingredients of local floras.

MEIOSIS IN RUBUS.

AUTO- OR ALLOPOLYPLOIDY.

Meiosis has been examined by the writer in more than 30 types. A few examples will be sufficient here, one diploid, one triploid, five tetraploids and two pentaploids of Moriferi veri, as well as the tetraploid *R. caesius*, three tetraploid and two pentaploid Corylifolii being dealt with.

The primary species, *R. tomentosus* BORKH., is, as mentioned previously, diploid and shows quite normally seven bivalents at diakinesis and first metaphase.

The triploid examined here is *R. nitidus* WHE et N. It behaves cytologically as a pronounced autotriploid. The number of trivalents is very high (on an average 4_{III} per cell, 8 good plates being analysed). From one to six univalents could be seen.

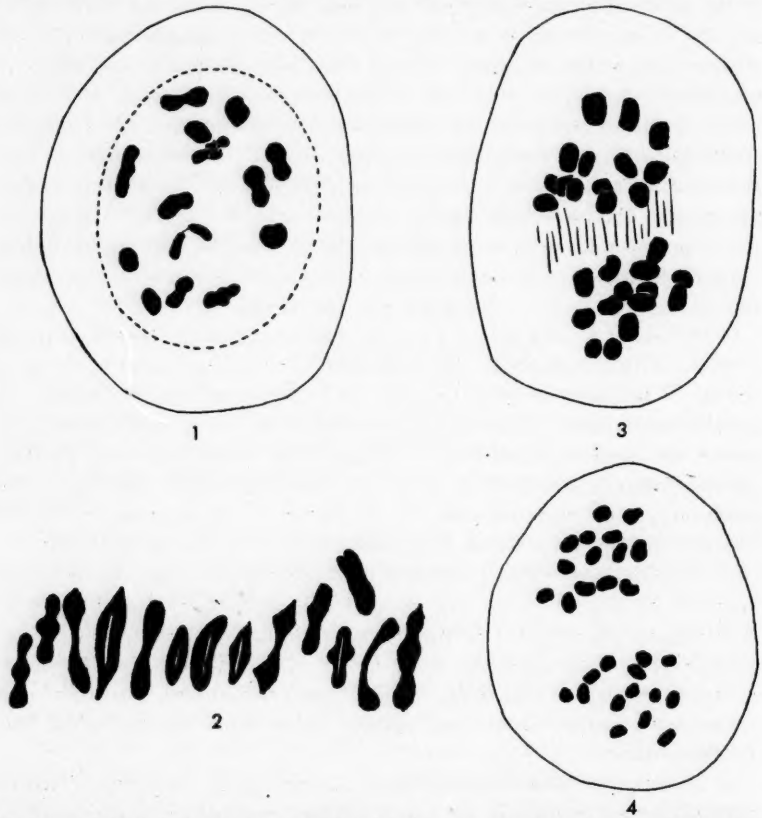
Of the five tetraploid Moriferi veri none is autopolyploid. Most commonly no more than one or two quadrivalents arise, most of the chromosomes pairing to form bivalents. *R. polyanthemus* LINDEB., *R. affinis* WHE et N., *R. vestitus* WHE et N., *R. armeniacus* F. and *R. hirtus* W. et K. produce $0{,}86_{IV}$, $0{,}67_{IV}$, $0{,}67_{IV}$, $1{,}00_{IV}$ and $0{,}06_{IV}$ per cell respectively. In order to arrive at a fairly certain estimate of the multivalent frequency the writer preferred to study diakinesis stages, since secondary associations occurring at first metaphase may render the analysis difficult and ring-quadrivalents in side-views of metaphase plates are occasionally counted as two bivalents. For the sake of completeness the data of *R. polyanthemus* and *hirtus* are submitted in full.

R. polyanthemus: 14_{II}, $1_{IV} + 12_{II}$ or 14_{II}, 14_{II}, $1_{IV} + 12_{II}$ or $2_{IV} + 10_{II}$, 14_{II}, $2_{IV} + 10_{II}$, 14_{II}, 14_{II} or $1_{IV} + 12_{II}$, 14_{II}, $1_{IV} + 12_{II}$, $1_{IV} + 12_{II}$, $2_{IV} + + 10_{II}$, $2_{IV} + 10_{II}$. *R. hirtus*: $1_{IV} + 2_{III} + 5_{II} + 8_{I}$, $1_{III} + 4_{II} + 11_{I}$ (incomplete), $5_{II} + 18_{I}$, $2_{III} + 5_{II} + 12_{I}$, $1_{III} + 6_{II} + 13_{I}$, $2_{III} + 7_{II} + 8_{I}$, $2—3_{II} + 22—24_{I}$, $3_{II} + 22_{I}$, $10—12_{II} + 4—8_{I}$, $6_{II} + 16_{I}$, $5_{II} + 18_{I}$, $3_{II} + 22_{I}$, $3_{III} + 5_{II} + 9_{I}$, $1_{III} + 8_{II} + 9_{I}$, $4_{II} + 20_{I}$. As meiosis in *Rubus* is studied only with difficulty, at least the first series does not claim to be entirely right. In *R. hirtus* unusually good diakineses with large nuclei and well-scattered chromosomes were found, and the configurations given above are no doubt rather correct. Cytologically, all five blackberries mentioned here must be regarded as (weak auto-) allopolyploids, this especially being the case with *R. hirtus*. Except for this type the pairing is normally very good, most of the chromosomes forming bivalents, univalents rarely occurring and when they do being few in number.

Meiosis of *R. Bellardii* WHE et N. was described in a previous paper (1933). In two completely analysed cells $1_{V} + 13_{II} + 4_{I}$ and $1_{V} + 1_{IV} + + 12_{II} + 2_{I}$ (or possibly $1_{V} + 2_{IV} + 10_{II} + 2_{I}$) were found. Studies on mitotic metaphases showed the occurrence of three satellite-chromosomes of a special appearance. These and other data indicate that cytologically *R. Bellardii* occupies a position between auto- and allopolyploidy. *R. vestervicensis* C. E. GUST. is of special interest in this connection, since it has been interpreted as a hybrid of *R. thyrsanthus* and *Bellardii*. The following meiotic configurations were found: $1_{IV} + 3_{III} + 11_{II} + 1_{I}$ or $1_{IV} + 3_{III} + 10_{II} + 2_{I}$, $2_{IV} + 1_{III} + 10_{II} + 4_{I}$, $1_{IV} + 1_{III} + 13_{II} + 2_{I}$, $1_{V} + 2_{III} + 10_{II} + 2_{I}$, $3_{IV} + 3_{III} + 5_{II} + 4_{I}$, $2_{IV} + + 1_{III} + 11_{II} + 2_{I}$, $2_{IV} + 3_{III} + 7_{II} + 4_{I}$, $1_{IV} + 2_{III} + 12_{II} + 1_{I}$, $1_{IV} + + 3_{III} + 11_{II}$, $1_{IV} + 1_{III} + 12_{II} + 1_{I}$. This type shows a rather high frequency of multivalents and appears to be more autopolyploid than *R. Bellardii*.

Studies on meiosis in *R. caesius* L. are highly important, THOMAS (1940) having published an interpretation concerning the connection of apomixis and autopolyploidy, partially founded on the supposed behåviour of this species. Three representatives, one from Bulgaria (scanty material) and two from the Lund Botanical Garden (spontaneous types), were examined. One of the Lund types in no instance produced quadrivalents or trivalents, either at diakinesis or at first metaphase (11 cells analysed). The anaphase separation proceeded regularly. The second Swedish type produced one quadrivalent in many diakineses and metaphases, but the occurrence of 14 bivalents was more frequent

($2_{IV} + 10_{II}$ or $1_{IV} + 12_{II}$; once, $1_{IV} + 12_{II}$; twice, $1_{IV} + 12_{II}$ or 14_{II}; three times, $1_{III} + 12_{II} + 1_{I}$; twice, 14_{II}; twelve times). The few irregularities occurring account for the slightly decreased pollen fertility, ± 90—95 % (cf. THOMAS, p. 127). Most probably *R. caesius* is an allotetraploid



Figs. 1—4. Meiosis in the ± allopolyploid *R. caesius* L. from the Lund Botanical Garden. Note that the almost complete apomixis of this circle species is accompanied by *allo*-polyploidy (cf. THOMAS, 1940). — 1. Transition stage of diakinesis and metaphase I. 14_{II}. — 2. Metaphase I. 14_{II}. — 3. Anaphase I. 14 + 14 chromosomes. — 4. Metaphase II. 14 + 14 chromosomes. — About 3200 ×.

species. The view will be expounded below that the origin of reciprocal translocations in biotypes propagating by apomixis may in the course of time alter an original allopolyploid into an apparent auto-allopolyploid, showing some multivalents at meiosis.

Like the tetraploid Moriferi veri, Rubi Corylifolii have a rather low frequency of multivalents. They differ, however, conspicuously by the frequent occurrence of univalents, although these are not entirely missing in the meiosis of Moriferi veri.

R. rosanthus LINDEB. var. *lejocarpus* LINDEB. gave in six PMC's the following configurations: $2_{III} + 9_{II} + 4_I$, $3_{III} + 8_{II} + 3_I$, $1_{III} + 9_{II} - 10_{II} + 4_I$ (incomplete), $1_{III} + 11_{II} + 3_I$, $3_{III} + 8_{II} + 3_I$, $1_{III} + 12_{II} + 1_I$, and 21 first metaphases (side views) contained on an average $2{,}86_I$ per cell. A specimen related to *R. dissimulans* LINDEB., growing in the Lund Botanical Garden under the name of *R. bahusiensis*, showed in three PMC's $13_{II} + 2_I$, $2_{III} + 8_{II} + 6_I$, $1_{III} + 8_{II} + 9_I$ and on an average $1{,}95_I$ per cell (this is a minimum number, 19 first metaphases). *R. centiformis* FRID. v. *Lidforssii* GEL. had in two completely analysed plates $1_{IV} + 1_{III} + 10_{II} + 1_I$, $1_{IV} + 3_{III} + 6_{II} + 3_I$. At first metaphase $1{,}00$ univalent occurred per cell (22 divisions). The configurations reported indicate that from a meiotic point of view none of the three Corylifolii is strictly allo- or autopolyploid but that a weak autopolyploidy bordering on allopolyploidy prevails.

The complete analysis of pentaploid Corylifolii is extremely difficult. Side views of first metaphase have in no case been analysed successfully. Polar views are somewhat easier to interpret, but owing to the phenomenon of secondary association the configurations do not reflect the true pairing. Diakinesis nuclei possess only infrequently such a size and structure as in Moriferi veri, thus rarely permitting of a complete analysis. Consequently, the data on multivalent frequency in *R. Wahlbergii* ARRH. are rather uncertain. If this reservation is borne in mind, however, they have some value. Fixations and analyses were made in two specimens (301 and 305) from Sweden, viz. Svanshall and Stenshuvud, both in Scania. A first metaphase of *301* was interpreted as showing $3_V + 3_{IV} + 1_{III} + 2_{II} + 1_I$. In 32 second divisions $0{,}6$ univalents per cell were excluded from the plates. In *315* one metaphase contained $4_{IV} + 1_{III} + 7_{II} + 2_I$ and three diakineses $3_{IV} + 2_{III} + 6_{II} + 5_I$, $1_{IV} + 1_{III} + 11_{II} + 6_I$, $3_{IV} + 10_{II} + 3_I$. 50 first metaphases gave an average number of $1{,}96$ univalents per cell. The high multivalent frequency is surprising. *R. Wahlbergii* approaches cytologically an autopolyploid constitution.

One specimen of *R. pruinosus* ARRH. may be included here. In this case the analysis was more successful. Seven PMC's contained $15_{II} + 5_I$, $3_{III} + 8_{II} + 2_I$ (incomplete), $1_{IV} + 2_{III} + 12_{II} + 1_I$, $1_{IV} + 13_{II} + 5_I$, $1_V + 2_{IV} + 2_{III} + 6_{II} + 4_I$, $5_{III} + 9_{II} + 2_I$, $1_{IV} + 2_{III} + 11_{II} + 3_I$.

50 first metaphases had a univalent frequency of 1,68 per cell. *R. pruinosus* occupies a position bordering on cytological autopolyploidy.

Summarizing the facts we may conclude: Triploid blackberries are from a cytological point of view strict autopolyploids. Tetraploid Moriferi veri behave as weak auto- or even allopolyploids. *R. caesius* is a ± strict allopolyploid. Tetraploid Corylifolii resemble the corresponding Moriferi veri in meiotic behaviour, but the univalent frequency is higher. Pentaploid Moriferi veri display a rather high formation of multivalents but cannot be regarded as strict autopolyploids. Pentaploid Corylifolii, especially *R. Wahlbergii*, behave as ± autopolyploids.

The opposite behaviour of tetraploids and of triploids and pentaploids *might* be interpreted in the following manner: The triploid and pentaploid complexes represent a more primitive state, as secondary crosses within them will take place to a less extent than among the tetraploids. The tetraploid blackberries, especially Corylifolii, proceed successively towards a condition of panmixis. Segregates or crosses which obtain another chromosome number in soma and consequently in gametes will tend to become isolated (*R. nitidus*, *Bellardii* and *Wahlbergii*). Their panmictic state will be less prominent.

As every Corylifolii-type has originated by a cross between *R. caesius* and Moriferi veri, it is from a *genetical* point of view allopolyploid. *R. caesius* differs morphologically from any true blackberry-type, no connections or transitions being known (except for the Corylifolii). Taxonomically it is isolated. The autopolyploid state of *R. Wahlbergii* is therefore nothing but a chimaera. That the chromosomes yet form multivalents, implies a restriction of the value of meiosis in proving *genetical* auto- or allopolyploidy. Nevertheless, the occurrence of multivalents in some blackberries in contrast to the exclusive formation of bivalents in others indicates that the apparent autopolyploids hold a more primitive position, the secondary processes of crossing being less pronounced.

Whether the triploids found to form a high number of trivalents at meiosis have once arisen as autopolyploids in the genetical sense, cannot be decided for certain. It must be stressed however that apomixis in *Rubus* implies a recessive condition. Thus the autotriploids cannot be the *immediate* products of a quantitative chromosome increase but should at least be segregates from such forms. This fact, as well as the lack of any similar or identical diploids (naturally these may be extinct), argues for an origin by more or less intense hybridization

followed by segregation processes, suddenly or gradually stabilizing the apomictic mode of propagation.

From the preceding data the conclusion is attained that apomixis is neither restricted to autopolyploid nor to allopolyploid forms in the cytological sense (compare *R. nitidus* and *Wahlbergii* with *R. hirtus* and *caesius*). THOMAS (1940) suggested that *R. nitidioides* and *thyrsiger* were autopolyploids, an interpretation which the writer cannot confute, but any attempt to associate apomixis with either of the two extremes of polyploidy will, as far as we know, be unsuccessful. This is true also of other genera. In *Hieracium* subg. *Archieracium* strict auto- as well as strict allopolyploids are found [according to the cytological analysis made by BERGMAN (1935 a) and GENTCHEFF and GUSTAFSSON (1940 a)]. In *Taraxacum* weak auto- and strict allopolyploids occur (GUSTAFSSON, 1935). In *Crepis* BABCOCK and STEBBINS (1938) discovered many gradations of auto- and allopolyploidy. According to FLOVIK (1938), at least part of the viviparous grasses are allopolyploids. In *Poa pratensis* and *alpina* a balanced condition of auto- and allopolyploidy prevails (MÜNTZING, 1940; ÅKERBERG, 1939, 1942).

Similar attempts to consider apomixis as a consequence of hybridization will probably fail. Apomixis is not restricted to hybridogenous complexes (cf. ERNST, 1918), nor is it, as DARLINGTON (1939) claims, »an escape from sterility». The results in *Rubus* and *Poa* prove that the apomictic propagation method gets lost in primary hybrids; consequently hybridization cannot by itself be the required foundation of apomixis. Moreover, the properties of derived sexuals in *Rubus* and *Poa* indicate that sexual biotypes occur within the amphi-apomictic populations and are in no way inferior to the apomicts, either in regard to vitality or to fertility, although they produce inconstant progenies.

POLLEN PROPERTIES.

STRUCTURAL DIFFERENTIATION.

The occurrence of diploid sexuals can, as mentioned previously, be settled on the basis of their regular pollen appearance, the uniform pollen size, and the small pollen diameter. By this means it will prove possible to confirm the general diploid state of a species or to pick out possible hybrids, misinterpreted types and — possibly — autotetraploid chromosome races from herbarium specimens. Five representatives of *R. ulmifolius* SCHOTT were investigated, collected in the Netherlands,

France and Algiers, every one having 100 % good grains and in three examined cases a pollen diameter of 16,50, 16,50, and 16,75 rel. units, i. e. much lower than in any case of triploids or tetraploids (10 rel. units = 15,4 μ). *R. incanescens* BERT. from Algiers had a pollen quality of 100 % and a pollen diameter of 14,70.

The triploid Moriferi veri examined in these respects, namely *R. nitidus*, *thyrsanthus*, *candicans* and *elatior*, are especially interesting,

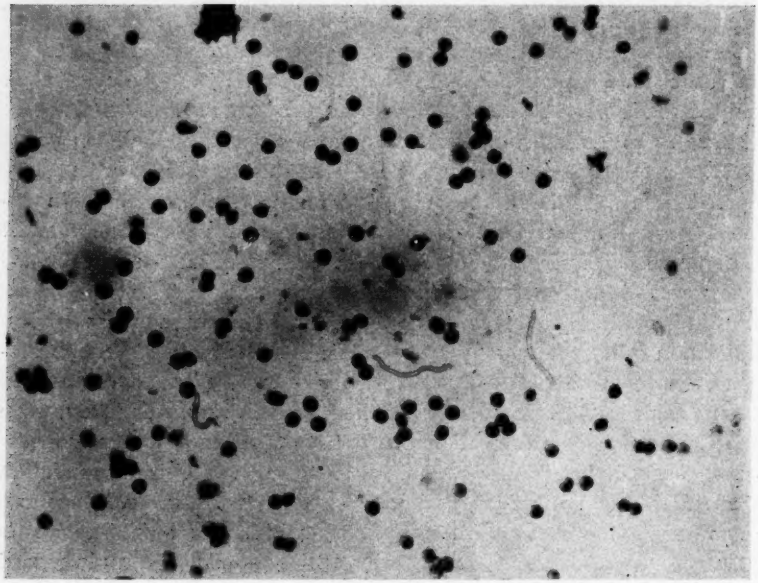


Fig. 5. The typical pollen appearance of a diploid circle species (*R. incanescens* BERT. Herbarium specimen. — Pollen containing about 100 % good grains. Diameter of the grains = 14,70 rel. units). — About 70 ×. Photo H. OLSSON, Svalöf.

as their pollen production is extremely poor. By the simple process of determining the percentage of good grains of a type known in part of its area to be triploid, we may find out whether it consists throughout of equal-chromosomed representatives. Tetraploid Moriferi veri have pollen of quite another appearance and size. One example of the usefulness of this method for studies on dried specimens will be presented below.

In his *Rubus* monograph SUDRE placed five minor species around the circle species of *R. nitidus* WHE et N., i. e. *R. nitidus* WHE et N.

(in the strict sense), *integribasis* MÜLL., *nitidiformis* SUD., *holerythros* F. and *indutus* BOUL. et VEND. *R. integribasis* is found in France, Germany, Belgium, Great Britain (possibly in Portugal), *R. nitidiformis* occurs in France and Germany, *R. indutus* in France and Germany, and *R. holerythros* in Germany, France and Great Britain. Concerning the distribution of *R. nitidus* reference should be made to p. 254. In the extensive *Rubus* herbarium gathered by Mr. C. E. GUSTAFSSON and

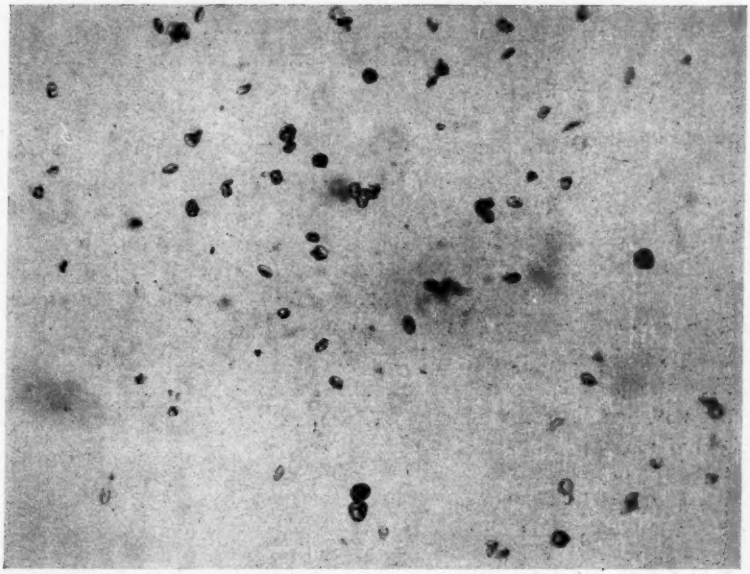


Fig. 6. The typical pollen appearance of a triploid biotype compound (*R. candicans* WHE et N. Herbarium specimen. — Pollen containing 11 % good grains. Diameter of the good grains = 17,35 rel. units). — About 70 ×. Photo H. OLSSON, Svalöf.

after his decease donated to the Botanical Museum of Lund University, 25 different specimens were examined (Table 1). In addition, an individual growing in Sweden (at Tranekärr in Scania) and having for certain 21 chromosomes, showed 9,7 % good grains. As immediately seen from the table, *R. nitidus* (in the strict sense) had, in all instances but one, a very poor pollen quality (0—10 %) and a fairly small pollen diameter. The single deviating specimen is wrongly named. The opposite behaviour of *R. integribasis*, *indutus* and *holerythros* is obvious. None of these has been determined as to chromosome number by direct counts, but their analogy in pollen properties to known tetra-

ploids and their difference from *R. nitidus* are too striking not to guarantee the supposed number of 2n = 28. Thus in 25 out of 26 cases it was possible to ascertain the chromosome numbers, but also in the exceptional case, *R. nitidiformis*, a probable number of 2n = 28 can be preliminarily accepted. In one case out of 19 in *R. nitidus* the taxonomical determination was incorrect. It is apparent that the pollen quality of the triploid *R. nitidus* cannot easily be increased above 10 %

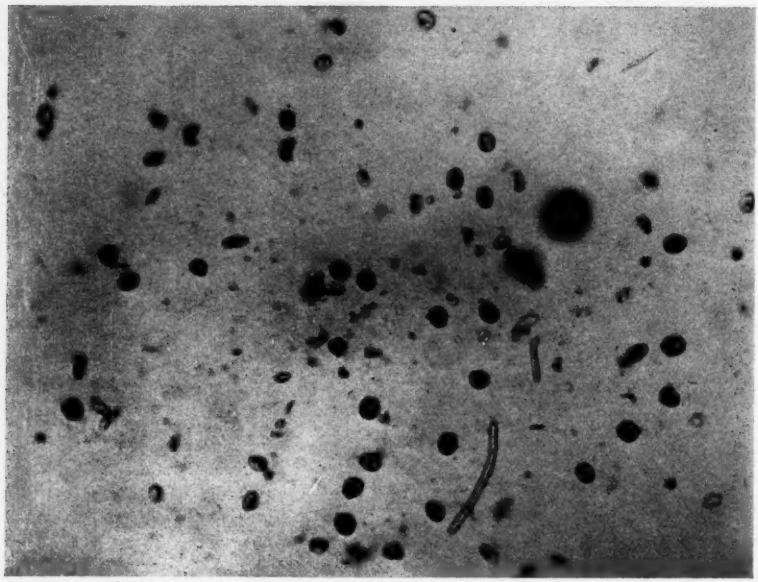


Fig. 7. The typical pollen appearance of a tetraploid biotype compound (*R. gratus* F. Herbarium specimen. — Pollen containing 73 % good grains. Diameter of the good grains = 21,65 rel. units). — About 70 ×. Photo H. OLSSON, Svalöf.

by external influences, a fact that does not imply however that types usually having good pollen cannot under certain environmental conditions produce poor grains.

An analysis like the one in *R. nitidus* and related types was performed in *R. thyrsoideus* (sp. coll.) and gave similar results. Also there a striking contrast exists between triploids and supposed tetraploids.

The tetraploid Moriferi veri have a superior pollen production. The pollen of *R. Scheutzii* LINDEB., *affinis* WHE et N., *scanicus* ARESCH.,

TABLE 1. *The chromosome numbers of R. nitidus* WHE *et* N. *and its relatives determined by pollen examination.*

Pollen No.	Name	Origin	Percentage good grains	Pollen diameter	Chromosome number
—	*R. nitidus* WHE et N.	Sweden	9,7 %	—	2n = 21
41	»	Switzerland	74,9 %	20,25	2n = 28! (Wrongly named)
42	» v. *hamulosus* LEF. et MÜLL.	France	6,5 %	19,80	2n = 21
43	»	Germany	0—5 %	—	2n = 21
44	» v. *hamulosus* LEF. et MÜLL.	»	3,2 %	19,60	2n = 21
45	» »	»	7,1 %	20,35	2n = 21
46	» »	France	0—5 %	20,60	2n = 21
47	» »	Germany	3,4 %	18,25	2n = 21
48	» »	»	3,4 %	19,40	2n = 21
49	» »	»	0—5 %	—	2n = 21
50	» v. *divaricatus* MÜLL.	France	3,5 %	19,05	2n = 21
51	» »	Germany	0—5 %	—	2n = 21
52	» »	»	0—5 %	18,90	2n = 21
53	» »	France	0—5 %	—	2n = 21
54	» »	Germany	0—5 %	19,75	2n = 21
55	» v. *oblongifrons* SUD.	France	5,1 %	18,30	2n = 21
56	» »	»	5,3 %	18,80	2n = 21
57	» v. *anglicanus* SUD.	England	0—5 %	—	2n = 21
58	» v.	France	0—5 %	—	2n = 21
59	*R. integribasis* MÜLL.....	Germany	40,6 %	20,65	2n = 28
60	»	Switzerland	69,3 %	20,40	2n = 28
61	» v. *pseudosulcatus* SUD.	France	57,8 %	20,15	2n = 28
62	» v. *latistipulatus* SUD.	»	68,9 %	21,45	2n = 28
63	*R. nitidiformis* SUD.	Germany	39,1 %	20,00	2n = 28(?)
64	*R. indutus* BOUL. et VEND. v. *crispifolius* GOETZ	France	57,6 %	—	2n = 28
65	*R. holerythros* F.	England	50,8 %	20,85	2n = 28

horridus HARTM., *sciaphilus* LGE and *gratus* F., all known as tetraploids, contain 66,8, 59,5, 64,6, 80,4, 77,3 and 77,0 % good grains respectively. Thus in no case of observed tetraploidy is the pollen constituted as in the triploids.

Three specimens of the pentaploid *R. Bellardii* WHE et N. were examined and showed a pollen production of 29,6, 78,2 and 58,5 % good grains. The individual variation is more conspicuous than in the tetra-

ploids. The variation in pollen *diameter* is more pronounced in the case of triploids and pentaploids than in tetraploids, a fact that provides another method of distinguishing tetra- and pentaploids in herbariums. The types known for certain as pentaploids are remarkably few in number: *R. vestervicensis* C. E. GUST., *kollundicola* C. E. GUST., *R. Bellardii* WHE et N. and *R. cordifolius* WHE et N. (a specimen cultivated in the Lund Botanical Garden), the first two being local forms. *R. Bellardii*, distributed all over Europe, may certainly be analysed in a manner similar to that of *R. nitidus* and *thyrsoideus*.

Thirteen specimens of *R. caesius* L., ancestor of all Corylifolii, have been analysed, the specimens having been collected in Sweden, Germany, the Netherlands, France, Moravia, Austria, Hungary, Bulgaria and Russia, twelve of them kept in the herbarium of the late C. E. GUSTAFSSON. If we exclude one specimen, which was incorrectly named, and three others, which gave an extremely poor pollen (almost 0 % good grains) owing to environmental conditions (shade, insect attacks, etc.), the nine remaining specimens showed 89,8, 87,4, 96,4, 38,7, 96,2, 92,6, 90,0, 95,8 and 96,8 % good grains, i. e. in general 90—95—100 % as stated by LIDFORSS in his experiments (1905, p. 9). The pollen diameter was on an average for 8 specimens 20,13 rel. units, approximately as in the tetraploid Moriferi veri, and well above that of diploids and triploids.

In the Corylifolii a singular status is met with. The tetraploid types have in most cases a poor pollen quality in contrast to the pentaploids, which are even better in this respect than several tetraploid Moriferi veri. *R. ciliatus* LINDEB. (4 specimens), *fioniae* FRID. v. *benefixus* C. E. GUST. (2 specimens), *R. acuminatus* LINDEB. = *gothicus* FRID. et GEL. (7 specimens), *R. centiformis* FRID. v. *Lidforssii* GEL. (2 specimens), *R. aureolus* ALL. (3 specimens), *R. glaucoformis* C. E. GUST. (2 specimens), *R. eluxatus* NEUM. (3 specimens) and *R. rosanthus* LINDEB. v. *lejocarpus* LINDEB. (2 specimens) have on an average 40,5, 24,3, 43,9, 25,7, 26,3, 12,7, 26,0 and 15,1 % good grains respectively.

The pentaploid complexes *R. Wahlbergii* ARRH., *pruinosus* ARRH. and *Lagerbergii* LINDEB. contain 71,1 % (7 specimens examined), 72,2 % (6 specimens) and 75,1 % good grains (2 specimens) respectively, the lowest individual percentage found being 54,8 % in contrast to the above-mentioned tetraploids, in which the highest percentage was 59,2 %. The pollen diameter of four tetraploids was 17,8, that of four pentaploids 20,88 rel. units, and thus here, too, the pollen diameter may furnish a valuable criterion of different chromosome numbers. In this way it will be possible to map the Scandinavian — and possibly

the extra-Scandinavian — Corylifolii correctly, at least with regard to any tetraploidy occurring (pentaploids and hexaploids have not so far been possible to distinguish by means of pollen quality and size).

As pointed out previously, the pentaploid Corylifolii represent a more closed system than the tetraploids, which are fundamentally panmictic. Owing to this property an accumulation of structural differences — deficiencies, inversions, translocations — is rendered possible in the tetraploids, where in the course of time many strikingly different genomes happen to combine. A secondary process, by which this structural differentiation will decrease, is the homozygotising that takes place in order to ensure the apomictic mode of propagation. Still, a complete homozygosity for structural differences is hardly possible in the few generations necessary. Crosses between widely different apomict-groups — as in the case of Rubi Corylifolii — will bring together chromosomes previously rearranged by translocations and inversions. Such chromosomes will form inversion-bridges and multivalents at meiosis, the latter simulating homology of entire chromosomes. Many tetraploids containing one or two quadrivalents at diakinesis and first metaphase may owe their ± weak autopolyploidy to crossings between structurally different types.

Inversion-bridges have been observed several times, in *R. nitidus* (second anaphase; note that this type is cytologically an autotriploid), *R. dasyphyllus* (first anaphase and second metaphase), *R. caesius* (first anaphase) and in *R. bahusiensis* (second anaphase). Previously the occurrence of inversion-bridges was noted in apomicts of *Crepis* (STEBBINS and JENKINS, 1939), in *Poa alpina* (MÜNTZING, 1940), in a sexual polyhaploid arisen from an apomict in *Poa pratensis* (loc. cit.), and in *Hieracium* subg. *Archieracium* (GENTCHEFF and GUSTAFSSON, 1940 a), where bridges and fragments frequently arose after special processes leading to a complete pairing. Inversion-bridges thus being known in several apomicts, the occurrence of translocations can also be postulated. In fact, these may be very frequent and they will influence the course of meiosis and pollen formation even more profoundly than do the inversions.

THE MECHANISM OF PSEUDOGAMY.

AUTOSEGREGATION.

Recent results obtained by NOACK (1939), GENTCHEFF and GUSTAFSSON (1940 b), TINNEY (1940), and ÅKERBERG (1942) render a new inter-

pretation possible of the mechanism of pseudogamy, and also of agamospermy as a whole. Two processes, 1) the origin of unreduced gametophytes and 2) the development of the unreduced egg-cells, are equally material in order to secure an apomictic propagation by means of parthenogenesis in phanerogams, but the single process *confined* to the apomicts is the autonomous embryo development. Parthenogenetic embryos may arise even in sexual species by certain ageing phenomena, when pollen cannot or does not fertilize the egg. But the phenomenon characteristic of obligate as well as habitual parthenogenesis in apomictic phanerogams is the more or less enhanced onset of embryo formation, as is established by studies in *Potentilla*, *Poa*, *Crepis* (STEBBINS and JENKINS, 1939), *Hieracium* (BERGMAN, 1935 a, 1941), *Ochna* (CHIARUGI and FRANCINI, 1930) and *Alchemilla* (MURBECK, 1901).

Unreduced embryo-sacs have been found in many cases of sexual propagation and are in fact so frequently reported that a complete list can hardly be made. In derived sexuals of *Poa pratensis* they are common (ÅKERBERG). The difference between apomicts and derived sexuals is — as far as we know — the incapacity of autonomous or at least early embryo development in sexual biotypes. The sexual egg-cell requires, or by means of a long dormant period it facilitates, the fertilization act prior to development. In several genera unreduced gametophytes arise, but in spite of the unreduced chromosome number their egg-cells cannot divide — not even after a prolonged period of ageing. Such instances are met with in *Artemisia* (CHIARUGI, 1926) and *Leontodon* (BERGMAN, 1935 b). They prove conclusively that the principal process in agamospermy as *propagation method* is the capacity of (autonomous) embryo formation.

The mechanism of the pseudogamy occurring in *Rubus* has not been worked out entirely, but the results obtained by CRANE and THOMAS (1940) and by the writer warrant a comparison with the conditions in *Potentilla*, *Poa* and *Hypericum*. The unreduced gametophyte in *Rubus* is formed by apospory (rarely by diplospory?), and the egg-cell develops without external stimulus autonomously, although in the scanty material hitherto obtained this process did not begin so early as in *Potentilla* and *Poa*. The difference between autonomous apomixis and pseudogamy is simply the necessity of fertilizing (or less probably stimulating) the fused polar nuclei in the latter case. Pseudogamy occupies an interesting middle-position of sexuality and autonomous apomixis, one part of the double fertilization act being suspended.

In the writer's opinion the autonomous parthenogenesis found in

many apomicts proves that the egg-cell division is not caused by external influences. Instead of that, the development is probably conditioned by a hormone regulation *within* the egg-cell, possibly by a co-operation of division-retarding and division-conditioning hormones. In the case of normal sexuality (the primary state) there *is* a certain time-dependence (haploid parthenogenesis). In sexual egg-cells the retarding hormones may disappear after fertilization or exceptionally by ageing, whereas in apomicts the division-conditioning hormones may set in shortly after the egg-cell is formed. In such species as *Artemisia nitida* and *Leontodon hispidus*, where egg-cell division cannot occur, the retarding hormones may be too powerful or the division hormones altogether destroyed. That the egg-cell development is not, as HABERLANDT declared (1921), conditioned by wound hormones, was shown in the needle experiments of KLING (1936) and is definitely determined by the phenomenon of pseudogamy.

New biotypes may arise from pseudogamous *Rubus* forms by the following methods:

A. By sexual propagation:

I. Without any change in the chromosome number.

a) The reduced egg-cell is fertilized by foreign pollen: true crosses (LIDFORSS; CRANE and THOMAS).

b) The reduced egg-cell is fertilized by pollen of same parent. Segregations are due to the heterozygous condition (LIDFORSS; CRANE and THOMAS).

II. The chromosome number is changed.

a) The reduced egg-cell is fertilized by reduced pollen, but one or the other of the two gametes contains an unbalanced chromosome number: monosomic types (microphyllus-forms) (CRANE and THOMAS), trisomic types: certain gigas-forms obtained by LIDFORSS?

b) An unreduced egg-cell becomes fertilized: *R. Borreri* f. hexaploida (CRANE and THOMAS), certain gigas-forms obtained by LIDFORSS?

B. By auto-segregation: The unreduced egg-cell develops parthenogenetically, but somehow a segregation of genes or whole chromosomes took place earlier in the normal or the aposporous EMC (LIDFORSS; DARROW and WALDO; CRANE and THOMAS).

C. By haploid parthenogenesis: *R. Borreri* f. triploida (CRANE and THOMAS).

D. By male parthenogenesis: *R. procerus* × Austin Thornless (DARROW and WALDO), certain triple species combinations carried out by LIDFORSS?

E. By vegetative bud-mutations (sports): *R. insularis, sciaphilus, laciniatus* and others (LIDFORSS; DARROW).

The phenomenon of autosegregation is specially worth discussing. The original case was described by LIDFORSS in 1907 (1907 a). He emasculated flowers of *R. insularis* and applied pollen from *R. caesius*. The offspring consisted with the exception of one plant of mother-like individuals, i. e. formed by pseudogamy. The exceptional plant differed conspicuously from the sister plants but showed no influence from the father (*R. caesius*). Several stem and leaf properties were altered. Concerning the origin of this form, it is most adequate, LIDFORSS says (1907 a, p. 5), to regard it »as arisen in the same way as the other false hybrids, i. e. asexually without any preceding nuclear fusion. In any case it is entirely hopeless to detect any morphological character which could indicate a blood relationship with *R. caesius*. The above assumption being correct, it is evident that the aberrant ought to be compared with the type of vegetative mutations known for a long time past as bud-mutations (sports)».

Further data were gathered by DARROW and WALDO (1933) and especially by CRANE and THOMAS (1939, 1940), the latter authors after crossing octoploid *R. vitifolius* with tetraploid *R. idaeus*, and *R. thyrsiger* with *R. nitidioides* and reciprocally. Some of the offspring consisted of true hybrids, others of mother-like individuals. The second group showed a conspicuous segregation, in the first cross with regard to sex and in all three crosses with regard to various morphological properties on stems and leaves.

The process of auto-segregation is of great theoretical significance, since it is the single means of biotype formation in apomictic groups with an entirely extinct sexuality. Unfortunately the embryological back-ground is unknown.

THE EQUILIBRIUM SYSTEM OF THE BLACKBERRIES.

The French batologist, H. SUDRE, gave in his monographical work »Rubi Europae» (1908—13) a more exhaustive account of the black-

berries than any previous scientist, even FOCKE not excluded, had been able to do. With reservation for all its mistakes (SUDRE knew only French blackberries from natural habitats and misinterpreted rather frequently those of other countries), the monograph is surprisingly reliable. Without difficulty all types named and described after the appearance of SUDRE's monograph can be included in his system.

In passing it must here be emphasized that the tedious — and by many hyper-scientists despised — study of the microspecies in polymorphous plant genera is by no means misspent. We obtain full information of the whole system, the »coenopopulation», exclusively by studying its constituents. »Our daily experience shows us that excessive analysis is far preferable to excessive synthesis» (LINDLEY, Syn. Brit. Fl., ed. I, pref. p. IX). The taxonomical method of pulverisation is an important tool by which to enrich our knowledge of the populations. Naturally the classification must not be ambiguous, nor the classifier himself ignorant. In the present writer's opinion SUDRE's system implies a distinct progress in comparison with earlier attempts, and is no doubt a starting-point for the future arrangement of our Rubi, even that of the miscredited Corylifolii.

The European blackberries form one single enormous population, characterized by morphological diversity, ecological differentiation and a great capacity of multiplication. The origin of new biotypes by means of hybridization is still conspicuous or, rather, it is in full progress. On the other hand, new forms arise rarely by a purely quantitative increase in chromosome number, in spite of the fact that all apomicts hitherto studied were polyploid. From the genetical point of view most blackberries should be regarded as allopolyploids, but cytologically many show a rather high frequency of multivalents, i. e. they simulate autopolyploidy.

The blackberries certainly form parts of a large population but it would be incorrect to assert that they constitute a continuous series from one extreme (Rubi Suberecti) to the other (Rubi Glandulosi). In fact, SUDRE's method of classifying the Rubi emanates from the circumstance, already shown by FOCKE in 1877 and 1902, that about 75 to 100 blackberry types are spread over large areas and at the same time are so distinct that a taxonomist can easily distinguish them from one another. Besides *R. caesius* (including the polymorphous Rubi Corylifolii) SUDRE proposed 109, what I call, circle species, divided into 4 subsectios, 14 series, and 22 subseries. Some of the circle species show no doubt such a restricted area of distribution that more properly they

should be withdrawn. Around the circle species the great mass of named blackberries may be grouped, several of which are similarly widely distributed, others comprise swarms of more or less unimportant forms and, thirdly, some merge into neighbouring circle species.

Within this population some primitive biotype compounds have been recognized. Every one is diploid, as far as is known also sexual, and shows a southern area of distribution. Some behave as relics, i. e. they have been forced into isolated districts (*R. Bollei* and *caucasicus*). But, on the other hand, two primitive circle species (*R. ulmifolius* and *tomentosus*) possess a wide Mediterranean and south-European distribution and are known to be polymorphous. A fifth primitive circle species, *R. incanescens*, occurs in the coastal area of southern France, of Spain, Italy and Algiers. In North-America sexual diploids are found, resembling the European Suberecti.

The apomicts, which form the major part of the blackberries and, in the same way as dandelions and hawk-weeds, are character-plants in the European flora, are in nature divided into two complexes: Moriferi veri and Rubi Corylifolii (cf. p. 249). The sexuals encountered belong to the former group. Corylifolii arose and still arise from crosses with *R. caesius*, which cannot be a primitive species in the same sense as the above-mentioned sexuals. Very probably the allotetraploid *R. caesius* originated from a diploid species hybrid after chromosome doubling. Its ancestors are, however, unknown and apparently extinct.

Moriferi veri are divided into various subsectios and series frequently having different centres of distribution. Southeast-European are Rubi Glandulosi, centring around the singular circle species *R. hirtus* and related to the sexual *R. caucasicus*. They are, however, also common in Switzerland and eastern France. In Great Britain the most abundant circle species and types belong to Discoloroides. In Scandinavia Suberecti and allied types form the bulk of blackberries, while Discoloroides, Discolores and Glandulosi are rather infrequent. This geographical differentiation partly depends upon an individual ecological response but for the greater part no doubt upon historical causes, i. e. an extreme mixis of genes and properties has not so far found sufficient time to occur. Evidently the blackberry population, in its entirety as well as in its local constituents, is in the act of a rapid transformation. At all events it is obvious that the Scandinavian *Rubus* flora will change greatly in the course of a few decades.

Among the Corylifolii, circle types (or circle species) have not been proposed so far, this partially owing to the fact that their nature of

hybrids and hybrid derivatives was recognized long ago, but partially also because they are unsatisfactorily known, more inconstant than Moriferi veri and pass over into each other. For the Scandinavian flora I propose a number of about fifteen circle types, to which different segregates and segregate compounds will be reckoned. Such circle types are, for instance, *R. pruinosus*, *dissimulans*, *rosanthus*, *ciliatus*, *fioniae*, *gothicus*, *Wahlbergii* and *cyclophyllus*. *R. pruinosus* is the circle type for the so-called Sub-Idaei, a member of which was synthesized by ROSANOVA (1938) in crossing *R. idaeus* with *R. caesius*. Owing to their inferior fruit-setting and to their inconstancy most Corylifolii are even more localized in distribution than Moriferi veri, but they possess the enormous power of vegetative propagation so characteristic of *R. caesius*. Therefore they form conspicuous mass formations in North-Europe.

The local floras are built up from circle species, crosses between them, and segregates of circle species and hybrids; those biotypes which are able to hold their own for a long time or even to spread, of course, being acclimatized to the local environments. When in future the features of the numerous local floras become known in detail, taxonomists should be able to agree upon a suitable number of standard types, the circle species, around which the almost inexhaustible mass of biotypes might be grouped.

No doubt a great number of local and widely distributed blackberry types are postglacial in origin, as some of them arose recently and new biotypes are continually produced. Some of the diploids encountered previously were regarded by FOCKE as relics from a Tertiary flora. Be that as it may, they certainly arose in preglacial or at least interglacial periods. Since some of them have a restricted area of distribution, cannot easily meet and consequently cannot hybridize, the combinations leading to the original polyploid apomicts should also be preglacial or interglacial in origin. Probably an interglacial blackberry flora existed, which became partially extinct during the last glaciation. Remnants of it survived and spread again when better conditions were established. The recent brambles are then the direct progenies and segregates from hybrids between them. Of course many types may also have arisen by new crossings with the primitive sexuals. The Corylifolii arise, disappear, or get absorbed in other Corylifolii, in the same degree as new Moriferi veri are formed, press forward, and get fertilized by *R. caesius*.

The great mass of Moriferi veri are tetraploid and in spite of all

outcrossings in the course of time have neither decreased nor increased their chromosome number. They have developed a special system of equilibrium characterized by two features, the disappearance of apomixis in hybridization and the recovery of apomixis in segregation. *In this manner the individual biotype compounds acquire a faculty of variation but at the same time maintain their quality of constancy.* Wherever two distinct and selectioned types happen to meet, they are able to create an enormous diversity of forms with new ecological and morphological properties via the F_1 hybrid. Some of these forms will prove to fit into the harsh conditions of nature, and consequently they will survive. Certainly not every two types which grow into each other are able to combine and form viable hybrids, but it is a noticeable fact that F_1 hybrids produced in experiments (LIDFORSS) frequently displayed a superior pollen production and were as vigorous as either parent. If one single F_1 shrub is formed, and if it succeeds in fructifying, it may for years continue to be the source of variations.

No apomictic circle species examined or any other known important type has lost its power of sexual egg-cell formation, with the possible exception of *R. caesius*, which in artificial crossings has so far given no hybrids as mother parent. Owing to its remarkably good pollen it has, however, served more than any other type as pollen parent, in nature as well as in experiments.

In the case of the Corylifolii the conditions are more complex, as hexaploid types are not infrequent, at least not in Atlantic regions. Nevertheless they possess similar properties, i. e. pseudogamy disappears in hybridization but reappears in segregation. Many hexaploids are extremely local. In fact, only one circle type is known that has the hexaploid number (*R. cyclophyllus*). Many inconstant forms having unequal-prickled stems and inflorescences also contain 42 somatic chromosomes. That they do not spread, depends either upon the fact that later on by chromosome elimination they turn into tetraploids, or that the hexaploid status itself involves an exceeding of the viability optimum. In this connection the point may once more be stressed that no hexaploid Moriferi veri are known from nature.

BABCOCK and STEBBINS (1938) and STEBBINS (1940) recently expressed the view that the apomictic systems, like polyploids in general, imply a »cul-de-sac» in evolution. A similar idea was also put forward by NANNFELDT (1938) in regard to polyploidy. It must be admitted that diploids cannot easily originate except from other diploids and that apomictic as well as sexual polyploids are certainly side-links of

normal diploids. In no respect, however, are the apomicts or the sexual polyploids unsuccessful in nature. In fact, they frequently appear to be superior in regard to spread and survival. This is evidently the case also in *Rubus*. Here the primitive species are extinct, relic, or have a southern distribution, in contrast to the apomicts which overflow great parts of the European continent. And the crucial point: The apomicts in *Rubus* have not lost their capacity of sexual seed production but take part in a prosperous equilibrium system of apomixis and sexuality.

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REDUCED PHALANGES AND CURLY COAT

TWO MUTANT CHARACTERS IN NATIVE SWEDISH CATTLE

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THE appearance in domestic mammals of new mutant characters in regard to hair and colour, skeletal build and conformation, and congenital defects is reported in the literature from time to time. In many cases the same, or a similar, mutant character may be found in different species, e. g. albinism in rabbits and cattle, woolly hair in swine and man, hairlessness in rabbits, dogs, swine, sheep and cattle, achondroplasia, amputated limbs, cleft palate and cryptorchism in swine, sheep and cattle, etc., suggesting that more or less homologous genes are affected. Available data indicate also that a certain mutation may occur repeatedly within the same species of farm animals. The same type of recessive achondroplasia has, for example, appeared in the Telemark breed of cattle in Norway, the Friesian cattle in Germany and Sweden, and in grade Jerseys and Guernseys of the United States (EATON, 1937; BRANDT, 1941).

It is of considerable interest that any finding of new mutant characters in domestic animals, or the independent occurrence of the same character in different breeds and localities, should be recorded in the scientific literature. For this reason the author presents the following description of two such characters which have appeared in the native cattle of the north of Sweden. None of the herds in which these characters were found contained any registered or tested cows, and no written records of the ancestry of the animals were kept, but owing to the fact that all the herds are small (2—8 cows), the owners are able to remember their individual cows and bulls for some time after having disposed of them. Mistakes may, of course, occur, but in most cases the information on the matings and parentage of the animals obtained by inquiry seemed dependable.

I. REDUCED PHALANGES (»CREEPER CALVES»).

In the spring of 1927 a county agent reported that »creeper calves» had been born in the village of Mockfjärd, province of Dalecarlia. The

calves were born at full term and they were said to be normal in every respect, except that the distal parts of the legs were shortened and deformed, which made it impossible for the animals to stand on their feet; they had to crawl in order to move about. The present writer was notified when another case of the same kind occurred, and made a trip to Mockfjärd in order to study the defective calves and find out as much as possible about their ancestry. Later on, new cases were reported from time to time by one of the Mockfjärd farmers, and three animals were sent to the Institute of Animal Breeding for examination. Thirteen cases in all were reported. The deformation of the legs was identical in the three animals, which were examined by the writer, and the other ten defective calves were said to be of the same type. The parents of the »creeper calves» were perfectly normal. The clear-cut manifestation of the character, and the fact that »creepers» appeared only after matings between related animals, suggested that the defect was hereditary and due to a recessive Mendelian factor.

The first defective calf examined showed a marked hypertrophy of the thyroid glands and had difficulties in breathing. It is not probable, however, that the goitre was correlated to the deformation of the legs, for the case in question was probably the only one in which a »creeper calf» had pronounced goitre. Reservation should perhaps be made for one stillborn calf in regard to which it was impossible to ascertain whether it was goitrous or not. It should be pointed out also that endemic goitre occurs in both domestic animals and man in the Mockfjärd district. Usually the »creepers» were vigorous and had a good appetite, but the first specimen sent to the Institute was near death at the time of examination. The legs were normal down to the carpal and tarsal regions, but the metacarpal and metatarsal bones were considerably shortened, and the first and second phalanges were entirely missing. The third phalanx, the hoofs and the tendons of the long digital extensor and deep flexor muscles were normal as well as the insertions of these tendons on the third phalanx. The skin and hair were also normally developed. The distal end of the metacarpal and metatarsal bones were separated half an inch from the third phalanx and connected with the latter only by the skin and tendons. The hoofs, therefore, appeared as loose appendages to the legs. When the animals tried to stand on their feet, the hoofs simply flapped aside, and the calves had to crawl on their knees and hocks.

Fig. 1 shows the skeletal parts of the right fore leg and hind leg. The former is shown largely from the lateral and the latter from the

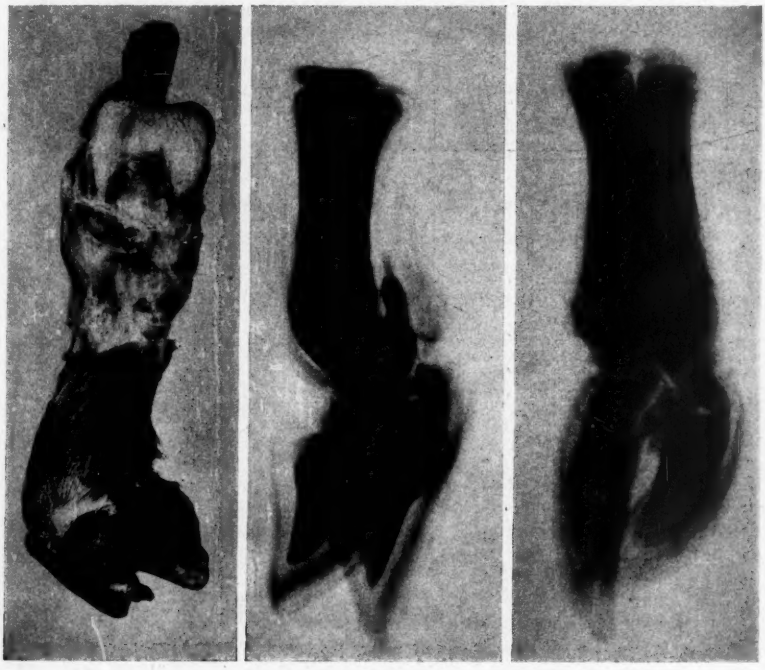
medial side; however, the carpal, metacarpal and metatarsal bones as well as phalanx III are viewed mainly from the front. The scapula and humerus, as well as femur and tibia, are normally developed, but the radius seems to be somewhat shortened. There was no fusion at all between the two metacarpal bones (Mc 3 and 4) but the two metatarsals (Mt 3 and 4) had started to fuse, although the fusion had not progressed very far. Small claws of approximately normal size were present. The figure gives an idea of the relative length of the different bones; of phalanx I and II no traces could be found. Fig. 2 *A* shows the frontal view of the right hind foot with the hoofs bent to the side, and *B* and *C* of the same figure present X-ray photographs of another right hind foot, *B* medial and *C* plantar view. The X-ray photographs show the bones in about $^2/_3$ of their natural size, but in picture *A* the foot is reduced to about $^1/_2$ of its size. The size of *A* is, therefore, not directly comparable with that of *B* and *C*. The small bones behind the distal end of the metatarsal bones and above phalanx III, which appear on the X-ray photographs, are the sesamoids. In all the animals examined, the defective leg development was of exactly the same type.

Fig. 1. Skeleton of the right hind (*A*) and fore (*B*) legs of a »creeper calf». The femur, tibia and tarsal bones are shown from the medial side, but scapula, humerus and radius-ulna from the lateral side; the carpal, metacarpal and metatarsal bones as well as phalanx III are viewed from the front.

The defect is probably due to an arrest of the skeletal development, occurring rather early during the fetal life. The »creeper calves» are quite different from the Dexter »bull-dogs» (CREW, 1924), or the recessive achondroplasts in other breeds of cattle, firstly because only the legs are affected, whereas the cranial skeleton is perfectly normal, and secondly because the arrest in the development of the legs is more clearly localized to a certain region than in the other two types. As far as the writer is aware no case of achondroplasia in mammals has been described, where certain bones of the appendicular skeleton are entirely missing while the proximal and most distal bones are normal,

as found in our »creeper calves»; the creeper fowl is also quite different (LANDAUER, 1934). The author desists from speculations in regard to the embryological interpretation of the skeletal defect, although it seems likely that the case may give some information on the sequence of the early development of the appendicular bones.

It was not possible to obtain complete information in regard to the



A *B* *C*

Fig. 2. Right hind foot of a »creeper calf»; *A* front view, *B* and *C* X-ray photographs (*B* medial and *C* plantar view). *B* and *C* show only the metatarsal bones, phalanges and sesamoids, but in *A* also the tarsal bones are left intact.

ancestry of all the »creeper calves», but the data that could be ascertained are summarized in the accompanying diagram (Fig. 3). The bull *A* produced in matings to related cows, probably half sisters, three »creeper calves», and his son, the bull *B*, produced six »creepers», four of which were carried by daughters of the sire *A*. The dams of the »creepers» 8 and 9 were also related to sire *B*, but the exact relationship was not known. All these nine »creepers» were born during 1926 and

1927. The sire *B* was butchered in June, 1927, and after that there was a pause in the production of »creepers» until November, 1930, when number 10 was born. This calf was sired by a son of *B*, the bull *C*, when mated to a paternal half sister. In 1934 the »creepers» 11, 12 and 13 were born by daughters of sire *B*, which had probably been mated to sire *C*, or possibly to a son of *C*. The same bulls had in matings to

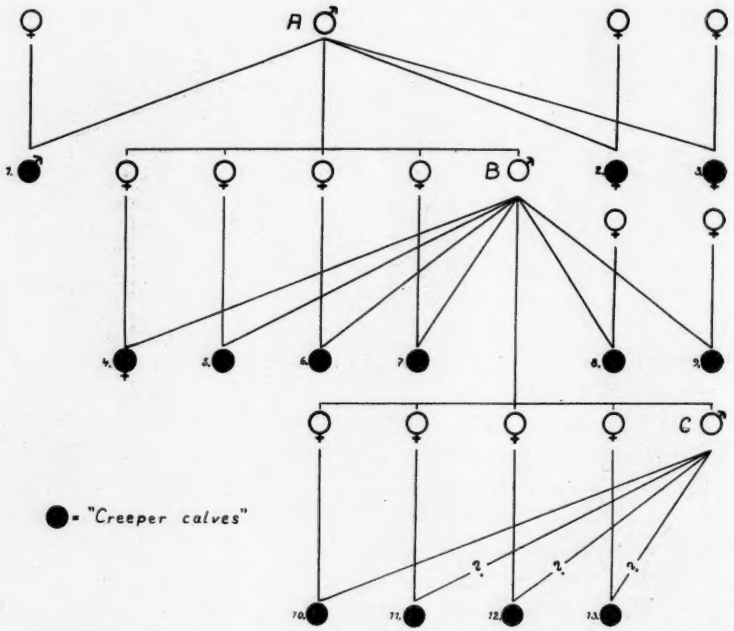


Fig. 3. Diagram showing the parentage of the »creeper calves» and the relationship between the parents, as far as it could be ascertained by inquiry among the owners of the herds. The sex of the »creepers» was known only in four cases.

the same cows also produced normal calves, but it was not possible to ascertain the exact number of normals, and therefore they are not shown in the diagram; consequently no ratio for normals to »creepers» can be given. Since 1934 no more births of defective calves have been recorded in the Mockfjärd district. The last bull by which they were sired was butchered, and new breeding bulls were bought from another district.

The facts presented above can probably be correctly explained on the assumption that the »creeper» character is caused by a recessive

gene in a homozygous condition, all parents of defective calves being heterozygotes. The gene may be classified among the lethals, or sub-lethals, because the »creeper calves» are viable only when they are subjected to special care. The calves were, as a rule, slaughtered at one or two weeks of age and were at that time in a perfectly healthy condition, but left to themselves they would have perished a few days after birth.

The history of the »creeper calves» is rather typical of that of any recessive lethal in a breed of farm animals. A mutation occurs, and the new gene spreads to a certain extent within the population, particularly through an extensive use of heterozygous bulls. When consanguineous matings are made, defective animals segregate out, and the segregates may in some herds or localities be rather frequent. However, the segregation continues, as a rule, only for a few years. If unrelated sires are introduced, it will probably cease altogether, and in more than 50 per cent of the cases any change of sire, even when the consanguineous matings are continued, will have the same effect. In order to reduce the risk of segregation of »creepers» all animals which have given rise to defective offspring should be excluded from further breeding. In the larger farm animals (horses and cattle) it is usually not practicable to make special tests of suspected sires by mating them to at least 20 of their own daughters, as suggested by WRIEDT and MOHR (1928), because this test would take too long time, and more trouble might be involved than the whole test is worth. In multiparous animals on the other hand, e. g. the pig, a test can be made quite easily by mating the sire to known heterozygous females (HALLQVIST, 1933).

The economic importance of the hereditary lethal characters in domestic animals has been exaggerated by some authors. The lethals are, of course, undesirable, and the breeders should be on their guard against them, but they do not represent any grave danger for our breeds or herds. When a lethal gene has gained a frequency level where repeated segregation takes place, it is extremely difficult to eliminate the gene altogether, but it is easy to reduce the frequency of segregates to a point where the segregation will be economically insignificant.

II. CURLY COAT (»KARAKUL CALVES»).

In the village of Edsbyn, Gävleborg's län, where neighbouring farmers market their products, it was observed that some of the calf and cow hides from a few remote farms were singularly curly coated

or woolly. Upon inquiry it was learned that cattle with this peculiar coat character had existed on the farms from a time about forty years ago, when the character was introduced by a bull from another district. In September, 1941, the writer made a trip to Edsbyn in order to study the animals and their breeding history.

At the time of my visit two cows were present on one farm, and one cow and a bull on another farm, all of which displayed the curly-coat

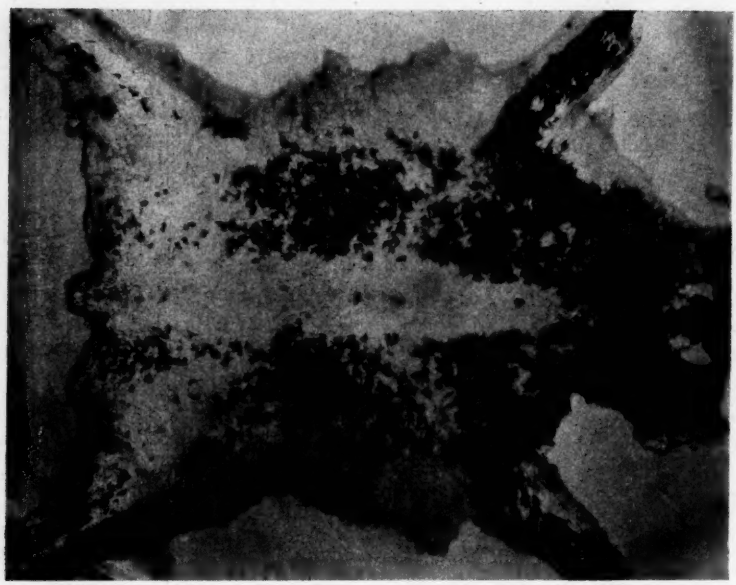
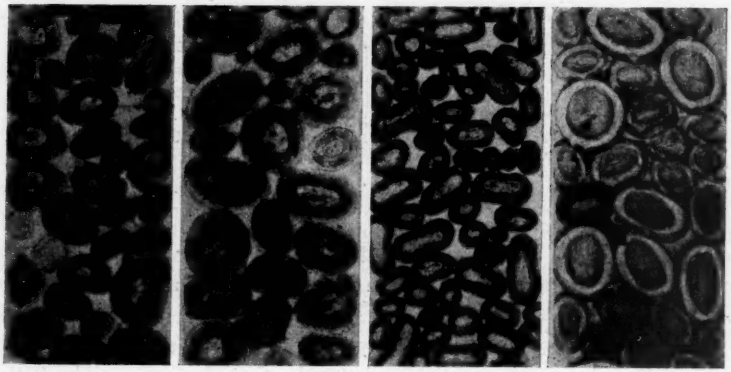


Fig. 4. The fur of a »Karakul calf» which was slaughtered at about two weeks of age.

character. The bull was about ten months old and of a dun colour; the cows had reached mature age. In regard to milking capacity and general vitality as well as conformation and colour they were typical of the polled cattle of northern Sweden. The hair was short and rather similar to a coarse and curly wool. This character of the coat was distinctly different from the normal type; mistakes in classification, therefore, seem to be excluded. Fig. 4 presents a picture of the coat of a calf which had been slaughtered at about two weeks of age. Here the curly character is very well developed, and the coat resembles that of a Karakul lamb. The writer has not examined the coat of a newborn calf of this type, but according to the statements of the farmers the

curls are usually tighter and more marked during the first days of life, similar to what is the case in the Karakuls. The hair of these calves was much coarser, however, than that of the Karakul lambs, and therefore the fur was not as beautiful.

The writer has examined hair samples of the curly coated bull and calf. The hairs of the ten months bull were rather fine with a narrow and discontinuous medulla; they were not uniform in thickness throughout their length, but thinner and thicker regions alternated. There was no clear difference between the hair of this bull and that of a normal animal of the same age in regard to the shape of the cross-sections



A *B* *C* *D*

Fig. 5. Sections of hair samples from the curly-coated bull and calf, compared with samples from normal animals of the same age. The samples were taken from the dorsal part of the chest region. Magnification × 106. — *A*. Curly coated bull. — *B*. Hair sample from a normal heifer of the same age as *A*. — *C*. »Karakul calf». — *D*. Hair sample from a normal calf of the same age and breed as *C*.

(Fig. 5 *A* and *B*), only in the diameter and size of the medulla. The hair of the curly coated calf was distinctly more flattened, however, than that of normal calves (Fig. 5 *C* and *D*); the transversal sections were elongated to an extent which is probably not found in normal hair. It is shown by several authors that woolly hair in man, Europeans as well as Negroes, is much more flattened than the straight hair type (MOHR, 1932; STEGGERDA, 1940). RHOAD (1934) found that woolly hair in swine is similarly flattened, and CRAFT and BLIZZARD (1934) made the same observation on »semi-hairless» cattle with curly hair. It would seem probable, therefore, that the hair sections in Fig. 5 *C* are typical

of the mutant curly coated calves in the polled Swedish cattle, although the writer has studied the hair of only one such calf.

The four curly coated animals which the writer inspected during his visit to the Edsbyn farms were all closely related. The two cows on one of the farms were dam and daughter, and the dam was maternal half sister to the curly coated cow on the other farm, which was the dam of the curly coated bull. The mother of the two dams mentioned had also been curly coated. All these mutant cows had been mated to bulls of the normal type; approximately half of the calves from these matings had a normal coat and half were curly coated. It was said that one of the cows had in matings to normal bulls produced 5 curly coated calves and no normals, but in all other cases the offspring were divided between both groups. As far as the farmers could remember, a curly coated calf had never appeared from a mating between two normal-coated parents. No matings between two curly coated animals could be placed on record, but only matings between normal and curly coated.

From what the writer was able to find out by inquiry it would appear that the curly-coat character is due to a dominant gene, and that all the four inspected animals are heterozygotes. Two of the animals, one cow and the bull, are now at the Skansen reservation of the Nordic Museum at Stockholm, where they will be mated to each other. It should be possible, therefore, to make an experimental study, on a small scale, of the genetics of the curly-coat character. The author is especially interested in the production of homozygotes in order to study the development of the character in these animals. It would seem probable that the »Karakul type» is more pronounced when the gene is present in the homozygous condition.

As far as the author is aware, this curly-coat character has not appeared among the cattle, native or import-descendants, in any other part of Sweden, and it is not similar to the recessive semi-hairlessness in Hereford cattle, described by CRAFT and BLIZZARD (1934). It resembles, however, an apparently dominant coat character found by KRONACHER (1924) in the German Fleckvieh, and may perhaps be identical with it. The curly coatedness in polled Swedish cattle is probably due to a gene mutation which had taken place many generations prior to that of the now living animals, but quite independently of a possibly identical mutation in German Fleckvieh. The author is not inclined to think that this type of curly coat in domestic cattle is an »original character» that can be traced back to the wild ox.

SUMMARY.

Two mutant characters are described which have occurred in native Swedish cattle. One is a congenital defect in the appendicular skeleton (reduced phalanges) with lethal, or sublethal, effect. The metacarpal and metatarsal bones are considerably shorter than in a normal animal, the phalanges I and II are entirely missing, but phalanx III and the hoofs are normal. The calves cannot stand on their feet, but crawl on knees and hocks (»creeper calves»). The other is a peculiar coat character which has no harmful effect on the vitality of the animals. In the newborn calf the hair is curly, as in a Karakul lamb, and in the adult it has a woolly appearance. The »creepers» and the curly coated calves appeared in different districts, and they were not related to one another.

No written records on the ancestry of the »creepers» and curly coated animals were available. From the information obtained upon inquiry among the owners of the herds where the characters occurred, the inference may be drawn, however, that the »creeper calves» are homozygous for a completely recessive gene, which probably has an inhibitory effect on the appendicular skeleton at an early stage of the embryonic development, and that the curly coat is produced by a dominant gene. The curly coat character will be subjected to further studies.

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CYTOGENETIC STUDIES IN RUMEX

III. SOME NOTES ON THE SCANDINAVIAN SPECIES OF THE GENUS

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THE first cytological examinations of the genus *Rumex* were made in the embryological works of FINK (1899), ROTH (1906) and DUDGEON (1918). Later investigations on the cytology of the species studied by these three embryologists have shown, however, that most of the chromosome numbers given by them must be regarded as wrong.

As the cytogenetics of this large genus has not previously been studied in connection with its taxonomy, the present writer began such investigations some years ago. The examinations deal firstly with the cytogenetic behaviour of the dioecious species found in Scandinavia, and secondly with the cytogenetics and taxonomy of the hermaphroditic species and the hybrids between them. Some results of the studies of the subgenus *Acetosella* have been given in previous papers (cf. LÖVE, 1941), and the taxonomy of the four species of this subgenus has been closely studied in connection with investigations of the cytology and genetics of this group (unpubl.). Studies on the cytology of plants from natural habitats have also been performed within the two other subgenera *Acetosa* and *Lapathum*, but as the hybrids produced within these two groups cannot be examined cytologically before the plants flower two or three years hence, it may be of interest to give an account of some of the results obtained.

Of *Rumex* subgenus *Acetosa* only three different species occur in Scandinavia. These are *R. scutatus*, which is found only in Upsala, where it may be regarded as adventitious, and the dioecious species *R. Acetosa* and *R. thyrsiflorus*.

The chromosome number of *R. scutatus* was firstly exactly determined by NODA (1926), who found the diploid number $2n = 20$ in plants from Japan, and by JARETZKY (1928) in Germany, who reported the same number. In England, however, FIKRY (1930) found the tetraploid number $2n = 40$. In the material from Upsala the number is $2n = 20$. Material of this collective species from different

localities in Europe will be studied cytologically and genetically, but up to now no tetraploids have been found in my material.

The polymorphous species *R. Acetosa* was studied by ROTH (1906), who found the haploid number n = 8 in the male individuals. As shown by KIHARA and ONO and others (cf. LÖVE, 1940), the diploid numbers are two in this species and in all other species of the section *Euacetosae*, which includes all the dioecious species of the subgenus, i.e. 2n = 14 in the female and 2n = 15 in the male individuals. The species and subspecies of *Euacetosae* found in Scandinavia are: *R. Acetosa* L. with the subspecies *pratensis* (WALLR.) BL. et D., *lapponicus* HIIT. and *fontano-paludosus* (KALELA) HYL. and *R. thyrsiflorus* FINGERH. In all these units some varieties and forms have been described, but in all plants studied by the present writer (from a great number of localities in Scandinavian countries and Iceland) the diploid number is 2n = 14 in the female and 2n = 15 in the male plants.

As reported by some Japanese workers (KIHARA and YAMAMOTO, 1931; YAMAMOTO, 1933, 1938; ONO, 1935), some different karyotypes are to be found in the species *R. Acetosa* and *R. montanus* in Japan. The plants studied there were of eight morphologically different karyotypes with differences in the geographical distribution (YAMAMOTO, 1938; cf. also ONO, 1935, p. 53). In my material of the different forms of *Euacetosae* found in Scandinavia and Iceland some karyotypes have also been found. Whether these karyotypes are to be regarded as fully identical with some of the Japanese ones is questionable, even if their morphology is at least almost identical with the figures given in the Japanese papers. Differences in the distribution of the different karyotypes in my material will be discussed in another publication later on. It may be mentioned, however, that it seems as if at least some of the karyotypes found may be connected with some taxonomical and ecological phenomena.

The studies on the cytology of *Euacetosae* deal mainly with the significance of the taxonomic differences in relation to the different karyotypes found within the species. A great number of crosses have been made between different karyotypes from different localities and also between the subspecies of *R. Acetosa* and *R. thyrsiflorus*. Up to the present no distinct differences have been detected between interspecific and intraspecific crosses, but further studies on the hybrids and the later generations may be of great interest for the cytogenetics and the taxonomy of the different forms. Fertile hybrids between the species *R. Acetosa* and *R. thyrsiflorus* may occur in nature, with pre-

dominance of some of the taxonomic characters typical of *R. thyrsiflorus*.

Triploid intersexes of *R. Acetosa* have been found in nature a few times. The first sterile intersex reported in the literature was detected by ROTH (1906), but its cytological behaviour was not investigated. In Japan, however, the genetical and cytological behaviour of the intersexes and their progeny have been closely studied by ONO (1935) and others (cf. LÖVE, 1940), and it has been demonstrated that all such individuals are triploids (or polyploids) with a disturbed balance between the X-chromosomes and the autosomes. In my material from Scandinavia no intersexual or polyploid plants of *R. Acetosa* have been observed, but in my material from Iceland one intersexual plant with the triploid chromosome number $2n = 22$ $(18\,A + 2\,X + 2\,Y)$ was found. This plant was almost fully sterile, but as a very low percentage of pollen grains was produced, some seeds were obtained after a cross-pollination with another plant from the same locality. Ten plants from this cross with the triploid intersex as father are being grown in the experimental fields, and nine plants from seeds from the triploid after open pollination are also being grown. After isolations of a great number of branches of the triploid only one — not fully developed — seed was obtained.

It is known from a great number of works (cf. LÖVE, 1940) that the sex-ratio of the species of *Euacetosae* does not follow the 1 : 1 proportion. On the whole it may be said that the proportion 100 females : ca. 40 males is the most frequent in nature. The reason for this disproportion is not known, but according to ROTH (1906) a part of it may be due to agamospermy (»apogamy») reported by him for *R. Acetosa*. However, the main cause of this disproportion may be differences in the growth rate of male and female determining pollen grains (cf. CORRENS, 1928). ROTH's results have not been controlled by later workers, but in *R. angiocarpus*, the diploid species of subgenus *Acetosella*, MURBECK (cf. NORDSTEDT, 1907) found some indications of agamospermy. As regards the occurrence of apomixis in *Rumex* and related genera, compare EDMAN (1929, 1931).

During two years the present writer has made a great number of absolutely safe isolations of female plants of *R. Acetosa* from different localities. Seeds were obtained from about 40 per cent. of the plants isolated. In most cases only one to ten seeds developed, but from some plants I obtained 20—25 seeds per isolation, and as many not fully developed seeds were found in a great number of cases. None

of my female diploid individuals have shown a tendency to develop anthers. The chromosome number of the plants from seeds produced without fertilization of female plants of *R. Acetosa* must be $2n = 14$ ($12\,A + 2\,X$) if diploid or $2n = 7$ ($6\,A + X$) if haploid, and at least all the diploid plants must be females. All the plants from the same mother plant must also belong to the same karyotype as the mother plant. So far none of these plants have flowered, but in the root-tip-cells studied only the diploid number $2n = 14$ has been counted, and no deviation from the maternal karyotype expected has been detected. Thus, *these observations strongly indicate the occurrence of agamospermy in my material of the dioecious species Rumex Acetosa.*

Plants isolated and pollinated with pollen grains from *Rheum undulatum* ($2n = 44$), *Rumex Acetosella* ($2n = 42$) and *Rumex tenuifolius* ($2n = 28$) gave a somewhat higher proportion of seeds than only isolated material. A wind-pollination of the plants is not fully excluded, and as only few somatic numbers of these plants have as yet been studied in order to see if different numbers occur in the progeny, it may be considered as somewhat doubtful whether a pollination with pollen from not closely related species may result in a greater number of agamospermous seeds. However, no hybrids between *R. Acetosa* and the three other species used for pollination have as yet been detected in the material.

Even if these results indicate that ROTH was right in his theory of the occurrence of apogamy in *Rumex Acetosa*, his hypothesis on the rôle of this for the sex-ratio found in nature within this and other species of *Euacetosae* may be wrong. In my material the highest sex-ratio may be ca. 100 : 40, i.e. ca. 70 per cent. females. If this disproportion was due only to agamospermy, this must occur in about 40 per cent. of the ovules. As every isolated stock normally without isolation produces at least some thousands of seeds, the agamospermy only occurs in 1—2 per cent. of the ovules of the plants which produced the greatest number of seeds per isolation. The plants pollinated with pollen grains from *Rheum*, *Rumex Acetosella* or *R. tenuifolius* gave a few more seeds, i.e. about 3—5 per cent. per pollination. A rather low percentage of the females may be produced by agamospermy, but the greater part of the disproportion is without doubt due to other factors, e.g. certation of male and female determining pollen tubes or other physiological or genetical phenomena.

The supposed agamospermy in *R. Acetosa* may be of the same character as the one found within some races of *Ranunculus acris*

(MARSDEN-JONES and TURRILL, 1935). In this species it »occurs in a low percentage of ovules, successfully in less than 1 per cent. under the most favourable experimental conditions tested». It may be of great interest to observe that the agamospermy is more frequent in some stocks of this species, as was also found by the present writer in the dioecious *R. Acetosa.* The occurrence of a low percentage of agamospermy may be rather frequent within a great number of Angiosperms, even if it has so far been detected only in a few species. It may be more frequent in the dioecious species than has as yet been observed.

Sometimes »viviparous» forms of female plants of the dioecious species of *Rumex* are met with in the herbaria. Instead of producing normal fruits, such plants at the first glance seem to have developed viviparous fruits »dropping» from the branches. On closer study, however, it is found that the plant is not viviparous but only monstrous. The pistils of the monstrous individuals are much enlarged after pollination, but hardly ever do they contain fully developed seeds. It seems as if the development of the seeds begins normally, but after some time the walls of the pistil become distended and split from the young seed, which dies.

In my material from Iceland one female plant was of this monstrous form. It was detected in the summer of 1940 and was crossed with a normal plant from Östersund, Sweden. Cytological analysis revealed no differences from the normal state. As this plant died in the cold winter of 1940—1941, it is no longer available for further study, but after a year or two five F_1 plants obtained and growing in the experimental fields will flower. A closer investigation of the genetic behaviour of this offspring and of plants of the same type, which are rather common in some parts of Iceland, is planned.

The studies of the subgenus *Lapathum* deal mainly with material of the species and hybrids between them found in nature and produced by experiment. This subgenus may be divided into three sections (cf. LÖVE, 1941), but only one of them, sect. *Simplices*, is represented in Scandinavia. The basic number of this section is $x = 10$ and polyploidy is rather common in the about 40 species as yet studied cytologically. Of these only about 15 per cent. are diploids, the others being polyploids with the tetraploid to 20-ploid numbers.

As the studies of the Scandinavian species and hybrids of this subgenus must be taken as preliminary experiments, only the chromosome numbers and some other minor observations will be reported here.

The chromosome numbers of the species, originating from different parts of Scandinavia, are: *Rumex conglomeratus*, *R. sanguineus* 2n = 20, *R. maritimus*, *R. palustris*, *R. obtusifolius* 2n = 40, *R. domesticus*, *R. crispus* 2n = 60, *R. Hydrolapathum*, *R. aquaticus*, *R. maximus* 2n = ca. 200. All the species, except the last-mentioned one, have been studied previously by other workers (JARETZKY, 1928; JENSEN, 1936; KIHARA and ONO, 1926). The number given here for *R. domesticus* was also found by KIHARA and ONO in material from Copenhagen, but in their material from Japan the octoploid number 2n = 80 was found. The hexaploid number 2n = 60 is found in all my material from different localities in Sweden and Iceland.

The species *Rumex maximus* has often been regarded as a hybrid between the two other 20-ploid species. As the chromosome number is the same and no distinct differences between the meiotic behaviour of this form and the other two high-polyploid species have been observed, it may be regarded as a distinct allopolyploid species as well as a hybrid. *R. maximus* is relatively fertile and gives rise to relatively constant offspring.

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SUMMARY.

1. The chromosome numbers of the Scandinavian species of *Rumex* are given. All the species and subspecies of subg. *Acetosa* sect. *Euacetosae* are diploid with 2n = 14 in the female, 2n = 15 in the male individuals. The material studied belongs to *R. Acetosa* ssp. *pratensis*, ssp. *lapponicus*, ssp. *fontano-paludosus* and *R. thyrsiflorus*. The Swedish material of *R. scutatus* is diploid with 2n = 20 chromosomes. The species of *Lapathum* studied have the chromosome numbers: 2n = 20, 40, 60, ca. 200.

2. The occurrence of karyotypes in *R. Acetosa* in Scandinavia is noted.

3. A triploid intersexual plant of *R. Acetosa* is reported from Iceland.

4. Some evidences are given as to the occurrence of agamospermy in the dioecious *R. Acetosa*. It may occur in some plants (40 per cent. of the plants studied) in a rather low frequency (1—2 per cent.).

5. The disproportion in the sex-ratio of *R. Acetosa* (100 females : ca. 40 males) may to a very small degree be caused by agamospermy.

6. A monstrous, »viviparous» form has been detected in the material from Iceland. No cytological differences from the normal forms could be detected in this plant.

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A NEW TRISOMIC MATTHIOLA TYPE

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IN the year 1936 Miss S. HASPERS found some plants of a highly deviating type in her *Matthiola* material (*M. incana* R. BR.) in the experimental garden of the Laboratory for Genetics, Wageningen. She was kind enough to submit the plants to me for further investigation, for which I wish to express my sincere thanks.

The composition of Miss HASPERS's material is evident from Table 1. The 7 deviating plants were thus found in three out of five F_3 families of a cross between two ever-sporting varieties, a nearly white flowered race (referred to as dirty white) and a red flowered one. The single-double ratio in these five F_3 families was as usual in ever-sporting families: of the normal plants 48,08 per cent were singles and 51,92 per cent doubles.

When observed for the first time in the late summer and autumn of 1936, the seven mutant plants had the characteristic appearance shown in Fig. 1: stout, fleshy stalks with many leaf-scars; at the top of each stalk a rosette-like group of densely arranged persistent leaves; the leaves have a slightly more fleshy and rigid appearance than in normal plants. The mutant (non-flowering) plants wintered in the green-house and were next spring replanted to the field. The formation of numerous short axillary sprouts caused the rosettes at the top of the stalks to become denser and heavier (Figs. 2 and 3). Of the seven mutants, six flowered in their second summer. Only one plant turned out to be a single, the remaining five were doubles (Figs. 2 and 3). Examination by the aceto-carmine method showed this single-flowering mutant to be a trisomic. Flower buds of this plant were fixed in Carnoy. The plant was isolated and produced small fruits, each with but a few seeds (Fig. 3). The seed was of a poor quality and showed a great variability in size.

These seeds were sown in April, 1938, in the green-house. Unfortunately, the percentage of germination was not determined. Some of the seedlings were small and weak. After a month, however, at the rosette stage in the open field, the differences in vigour had almost disappeared. At this stage plants later found to be trisomics were

almost or entirely indistinguishable from normal plants. During the months June and July differences became extremely clear. The

TABLE 1. *The Matthiola material in which the mutant type was found.*

	Family	Singles	Doubles	Mutants	Total
1.	Dirty white, selfed	41	70	0	111
2.	Dirty white × red	25	33	0	58
3.	Red, selfed	46	56	0	102
4.	Red × dirty white	47	64	0	111
5.	F_3 family	129	121	0	250
7.	» »	87	88	2	177
8.	» »	74	101	2	177
9.	» »	167	153	0	320
11.	» »	155	198	3	356
	Total of all F_3 families:	612	661	7	1280

mutant type remained at a many-leaved rosette stage (the type may be called »Rosette»). Not until the end of July, when the normal plants

Fig. 1 (to the left). Autumn of 1936. Non-flowering trisomic plant. — Fig. 2 (to the right). Summer of 1937. The only single-flowered trisomic plant.

flowered and fruited profusely, did the supposed trisomics begin to produce their fleshy, densely leaved stalks (Fig. 4). The whole family consisted of 135 plants, viz. 102 singles, 11 doubles, and 22 non-

Fig. 3. Autumn of 1937. To the left: the same trisomic plant as in Fig. 2, now bearing small, few-seeded fruits (the greater part of the plant was used for making cuttings, although without result). To the right: the same trisomic plant as in Fig. 1, double-flowered with but one small raceme (its stalks had to be supported because of the heavy load at their tops).

Fig. 4. Summer of 1938. Offspring of the single-flowered trisomic; three trisomic plants between some normal ones.

flowering Rosettes. With these latter plants a more accurate investigation was planned, but, unfortunately, all died in the beginning of the winter because they were kept in too moist a place.

That these 22 non-flowering plants in all probability must be considered as trisomics follows from their similarity to the original mutants. Moreover, root tips were fixed from plants 1—14 and flower buds from plants 1, 2, 6 and 13. Of these fourteen plants, Nos. 3 and 11 were found to belong to the non-flowering Rosette type. The tips of No. 3 showed a very poor fixation and no countable plates; No. 11 clearly showed 15 chromosomes. The root tips and p. m. c.'s of the remaining twelve (normal) plants all possessed 14 chromosomes.

As fixation was not very satisfactory, only very few good trisomic somatic plates were found and a complete analysis of the genome was impossible. In the plates represented by Figs. 5 and 6, however, seven chromosomes with clear median or submedian spindle insertions were found; the remaining eight seemed to have one arm much shorter than the other one. The extra-chromosome therefore was supposed to be of the median or submedian type. This supposition was corroborated by studies of meiosis.

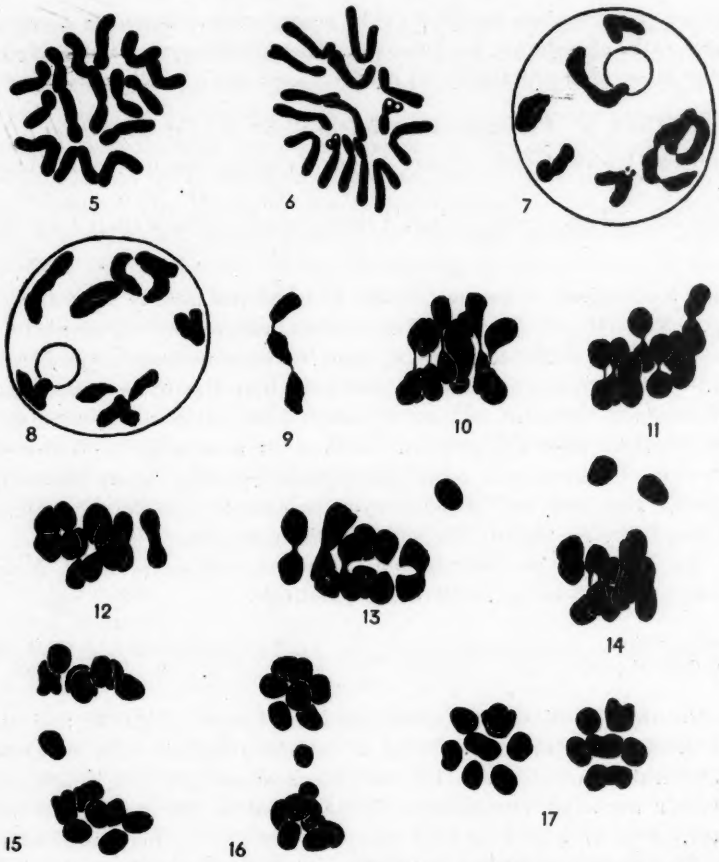
Meiosis in the normal plants was found to be regular, but was not studied in detail. Of the trisomic mother plant diakinesis, the first metaphase and first anaphase were studied.

Diakinesis is represented by Figs. 7—9. The cell in Fig. 7 shows a chain trivalent, that in Fig. 8 a univalent. Fig. 9 represents a chain trivalent, separately drawn. Differences in size between the three homologues do not exist or are at any rate inconspicuous. Moreover, it is clear from Figs. 7 and 8 that the chromosome concerned does not belong to the largest size class: in at least two chromosome pairs the chromosomes are larger (see Discussion). 36 diakinesis cells were completely analysed, their configurations being shown in Table 2 (trivalents, rings, rods, and univalents). Only one trivalent was of the frying-pan type (⌒—), all the others were chains (— — —).

TABLE 2. *Chromosome configurations at diakinesis.*

With one trivalent and:	4 rings	3 rings	2 rings	1 ring	0 rings	total cells
	1	4	6	11	0	22
With one univalent and:	**4 rings**	**3 rings**	**2 rings**	**1 ring**	**0 rings**	**total cells**
	1	2	9	2	0	14

I—M plates in side-view are represented by Figs. 10—14. The metaphase chromosomes are very short and round and therefore



Figs. 5—17. Cytology of the trisomic *Matthiola*. (Magnification ± 3450 ×.) — Figs. 5—6, somatic metaphase plates; Fig. 5, from an ovary wall of the trisomic mother plant; Fig. 6, from a root tip of a trisomic daughter plant. — Figs. 7—17, first meiotic division in the p. m. c. — Figs. 7—9, diakinesis; Fig. 7, $1_{III} + 2\ ring_{II} + + 4\ rod_{II}$; Fig. 8, $2\ ring_{II} + 5\ rod_{II} + 1_I$; Fig. 9, a separately drawn trivalent. — Figs. 10—14, first metaphase; Fig. 10, 1 zig-zag$_{III}$ + 1 ring$_{II}$ + 5 rod$_{II}$; Fig. 11, 1 non-zig-zag$_{III}$ + 2 ring$_{II}$ + 4 rod$_{II}$; Fig. 12, 1 frying-pan$_{III}$ + 2 ring$_{II}$ + 4 rod$_{II}$; Fig. 13, 3 (?) ring$_{II}$ + 4 rod$_{II}$ + 1$_I$; Fig. 14, 1 zig-zag$_{III}$ + 2 ring$_{II}$ + 3 rod$_{II}$ + 2$_I$. — Figs. 15—17, first anaphase; Fig. 15, side-view with a lagging univalent; Fig. 16, side-view with a divided univalent; Fig. 17, polar view, in each group two big chromosomes with ± median spindle insertion.

difficult to study in detail. Still, from such trivalent structures as seen in Figs. 10 and 14 it is evident that the chromosome concerned has a

median or submedian insertion. The configurations found in 80 metaphase cells are shown in Table 3. The chromosomes not included in the table were practically all rod bivalents, only 3 cells possessing 2,

TABLE 3. *Chromosome configurations at first metaphase.*

With one trivalent and:	4 rings	3 rings	2 rings	1 ring	0 rings	total cells
		5	15	18	3	41
With one univalent and:	**4 rings**	**3 rings**	**2 rings**	**1 ring**	**0 rings**	**total cells**
	1	10	20	7	1	39

2 and 3 univalents respectively. The 41 trivalents were of the following types: 33 ⌒. 6 | and 2 ⊂ —. The average number of ring bivalents in the cells with a trivalent is 1,54, that in those without a trivalent is 2,08. This difference makes it probable that the three homologous chromosomes in cells without a trivalent are often represented as a ring bivalent plus a univalent. This is in agreement with the observation of a median or submedian spindle insertion (sharp distinction between ring and rod bivalents was impossible; the actual numbers of rings may be slightly higher than those mentioned above).

In 150 cells the distribution of the chromosomes at I—A was studied, the following result being obtained:

Configuration :	8+7	7+1+7	8+1+6	7+2 halves +7	total cells
Number of cells:	140	6	1	3	150

Thus, only 7 cells showed a lagging chromosome (Fig. 15) and only 3 a divided one (Fig. 16). In 14 of the 150 anaphase cells difficulties of separation were shown by one chromosome pair. It is unknown whether the same chromosome is concerned in all or most of these cases. Fig. 17 depicts a I—A in polar view. Two big chromosomes can be seen in each group, one in the centre and the other at 12 o'clock. Apparently they have ± median spindle insertions and are previous partners of ring bivalents. In all probability the same big chromosomes are to be seen at diakinesis (Figs. 7 and 8; a ring and a rod in each).

DISCUSSION.

All *Matthiola* trisomics hitherto described were found by FROST in the double throwing variety »Snowflake» (FROST, 1919, 1921, 1927, 1928, 1931; FROST and MANN, 1924). That variety produces every year between 2 and 5 per cent such mutants. This high percentage of chromosome mutants undoubtedly has some connection with a

cytological peculiarity of the Snowflake variety (MANN LESLEY and FROST, 1927). It has chromosomes which are remarkably long at the late prophase and the metaphase of the first meiotic division in the p. m. c. Abnormal cytological behaviour responsible for the production of the trisomic mutants very often occurs in this long chromosome variety, whereas it is extremely rare in plants with normal short chromosomes. The plants of the material described in the present article belong, as far as investigated, to the short chromosome type. At present the cytological causes underlying the production of the trisomic plants in this material are unknown.

Leaving double trisomics and tetrasomics out of consideration, eight different trisomic types have so far been described in *Matthiola*. Four of them are considered by FROST to be primary trisomics, the remaining ones being secondary trisomics. On the basis of morphological, cytological or genetical indications FROST tentatively associated the secondaries with the primaries as follows.

Primary trisomics	Corresponding secondary trisomics
Crenate	Slender (fragment) and Crenatoid
Dark	Large (»)
Smooth	Small (»)
Narrow	

It is rather certain that the Rosette type described in the present paper is not identical with any of these types.

In the offspring of the Crenate trisomic (and of Slender also) FROST established a clear »linkage» of trisomic with singleness and of normal with doubleness. He concludes that the triple chromosome concerned is that which carries the factor pair for single (*S*)—double (*s*) flowers (and the pollen-lethal factor pair linked with it). The constitution of Crenate is, according to FROST, *Sss*, the chromosome with the factor for singleness (and with the lethal factor) being represented only once.

The offspring from the trisomic Rosette described here shows a reversed association (at least among the normal plants; the trisomics died before flowering): 22 trisomics, 102 normal singles and 11 normal doubles being obtained. One might suppose this to depend upon the constitution *SSs*, the chromosome with the factor for singleness (and the lethal factor) being represented twice. With random chromosome assortment such a plant would produce four types of egg-cells, viz. 1 *s*, 2 *Ss*, 2 *S* and 1 *SS*, and probably two viable types of pollen, 1 *s* and 2 *Ss*. Excluding other selective influences, and assuming that

tetrasomics are non-viable, this would result in an offspring consisting of 9 trisomic singles, 0 trisomic doubles, 2 normal singles, and 1 normal double (or, with only *s* as functional pollen: 3, 0, 2, and 1 respectively). The numbers actually obtained deviate highly from these expected numbers. Moreover, the Crenate type of FROST is not identical with the Rosette type. In view of the scanty material and the many complications in *Matthiola* trisomics a more detailed discussion seems hardly advisable at the moment.

The chromosomes of *Matthiola* were studied by ALLEN (1924). Their diploid number is 14 and, according to ALLEN, there is no morphological dissimilarity between the chromosomes, all of which are U or V shaped. PHILP and HUSKINS (1931), however, think it possible to distinguish each of the seven pairs, and ARMSTRONG and HUSKINS (1934) come to about the same result. According to the last mentioned authors, the seven chromosomes, indicated by PHILP and HUSKINS with the letters A—G, can be characterized as follows:

A.	Long; subterminal spindle insertion	
B.	Long; median » »	difficult to distinguish (B slightly longer, according to PHILP)
C.	Long; median » »	
D.	Medium; subterminal » »	
E.	Medium; submedian » »	difficult to distinguish
F.	Medium; median » »	
G.	Short; subterminal » »	

According to PHILP (PHILP and HUSKINS, 1931), the triple chromosome in Crenate is A [1]. Chromosome E is described by PHILP as having an almost median spindle insertion, ARMSTRONG and HUSKINS describe it as submedian, and KUHN (1938) writes: »Dieses Chromosom scheint sehr häufig nicht in der Mitte, sondern an einer submedianen bis subterminalen Stelle eingeknickt zu sein».

In my own material it was impossible to identify each chromosome. In a few mitotic plates, however, seven chromosomes with two equal or sub-equal arms could be distinguished (Figs. 5 and 6). They probably represent the chromosomes B, C (both long) and F (medium). As shown in the description of the meiotic division, the triple chromosome is of medium size and has median or submedian spindle insertion. From these facts it would seem very probable that F is the

[1] The small satellite of this chromosome described by PHILP and HUSKINS (1931; cf. also WESTERGAARD, 1936 and KUHN, 1938) was, owing to the less good fixation, not visible in my material.

chromosome concerned in the production of the trisomic Rosette type of *Matthiola* (or possibly E, which chromosome differs but slightly from F).

SUMMARY.

A trisomic ever-segregating *Matthiola* type, indicated as Rosette, is described. The offspring of a single-flowered trisomic plant after selfing consisted of 22 trisomics, 102 normal singles and 11 normal doubles.

The triple chromosome is of medium size and has a median or submedian spindle insertion. Probably it corresponds to the chromosome indicated by the various authors with the letter F.

The triple chromosome was represented as a trivalent in 22 out of 36 diakinesis cells and in 41 out of 80 first metaphases. The trivalent structure almost always occurs as a chain.

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CYTOLOGICAL STUDIES OF TRIPLOID PROGENIES OF POPULUS TREMULA

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TWO years ago the writer submitted some data concerning the occurrence of triploid races of *Populus tremula*, crosses between diploid and triploid races being also dealt with (JOHNSSON, 1940). It was then shown that nine different clones of triploid aspen are known in Sweden. Both male and female clones occur. The chromosome number of *P. tremula* is $x = 19$. Meiosis in the triploids shows at IM trivalents, bivalents and univalents and gives rise to gametes with chromosome numbers varying between 19 and 38. Further, unreduced gametes with $n = 57$ are formed. Crosses between diploid and triploid races are noteworthy in that individuals with aneuploid chromosome numbers are realized in high frequency, in which respect *Populus tremula* differs markedly from nearly all species in which 2x—3x crosses have been investigated. Crosses in both directions gave the same results, thus showing that the pollen grains are not more susceptible to numerically unbalanced chromosome numbers than the embryo-sacs. These studies have, however, been extended to embrace also crosses triploid × triploid, the results of which are submitted as a supplement to the earlier account of crosses diploid × triploid.

Diploid × triploid crosses. — As there is now available a far larger material of the combination diploid × triploid than that published in 1940, it may be justifiable to submit an analysis of the material as a whole, especially as the chromosome numbers have been determined for in all no fewer than 1,665 F_1 individuals. This analysis is given in the form of a diagram, Fig. 1, in which the broken line indicates the percentage distribution of F_1 individuals with different chromosome numbers from 47 different crosses diploid × triploid and reciprocally. This curve agrees almost entirely with that recorded in 1940 and based on a considerably smaller material. The only difference is that the curve has now received a more even course, a number of random irregularities having been eliminated. The mean of the chromosome numbers of 1,635 individuals (the tetraploid and approximately tetraploid have not been included) is 46,7 as compared with 46,3 for 617 individuals in 1940.

Triploid × triploid crosses. — Four crosses between triploid and triploid aspen have been made. The fertility of the crosses is low both as compared with crosses between diploids and as compared with crosses in which only one of the parents is triploid. The fertility of the crosses and the germinability of the seed were as follows:

Type of cross	2x × 2x	3x × 2x	3x × 3x
Number of crosses	18	5	4
» » seeds per capsule	9,9	4,3	2,4
Germinability of seed	94 %	45 %	48 %

In this comparison the triploid parents in the 5 crosses 3x × 2x are the same triploid ♀-individuals as those employed in the 3x × 3x crosses. The low seed setting in the cross triploid × diploid as compared with diploid × diploid crosses must be due to a great many of the ovules of the diploid aborting, either as the result of the lethal constitution of the haploid (n-) egg-cell or on account of diploid (2n-) lethal combinations arising at fertilization. The further reduction of the seed setting occurring in the cross triploid × triploid must be due to an increased frequency of lethal diploid (2n-) combinations arising on fertilization.

Chromosome numbers of the triploid offspring. — The chromosome numbers have been determined for 308 individuals from the four triploid progenies, the following distributions being obtained:

2n =	38	39	40	41	42	43	44	45	46	47
Number of individuals	17	3	2	4	5	6	1	5	10	11
2n =	48	49	50	51	52	53	54	55	56	57
Number of individuals	11	8	11	4	11	13	12	23	21	56
2n =	58	59	60	61	62	63	64	65	66	67
Number of individuals	13	15	3	5	6	9	1	8	3	0
2n =	68	69	70	71	72	73	74	75	76	
Number of individuals	3	1	0	3	0	1	0	1	2	Total 308

In the diagram, Fig. 1, a corresponding curve has been drawn (the unbroken line) after conversion to percentage of the total number of individuals. The most characteristic features of the curve are that practically all theoretically possible chromosome numbers are realized, and that there is a pronounced maximum for the triploid number, n = 57. This maximum corresponds to the class which in respect of the chromosome numbers of the gametes (JOHNSSON, 1940) should be most numerously represented if no special selective mechanism is

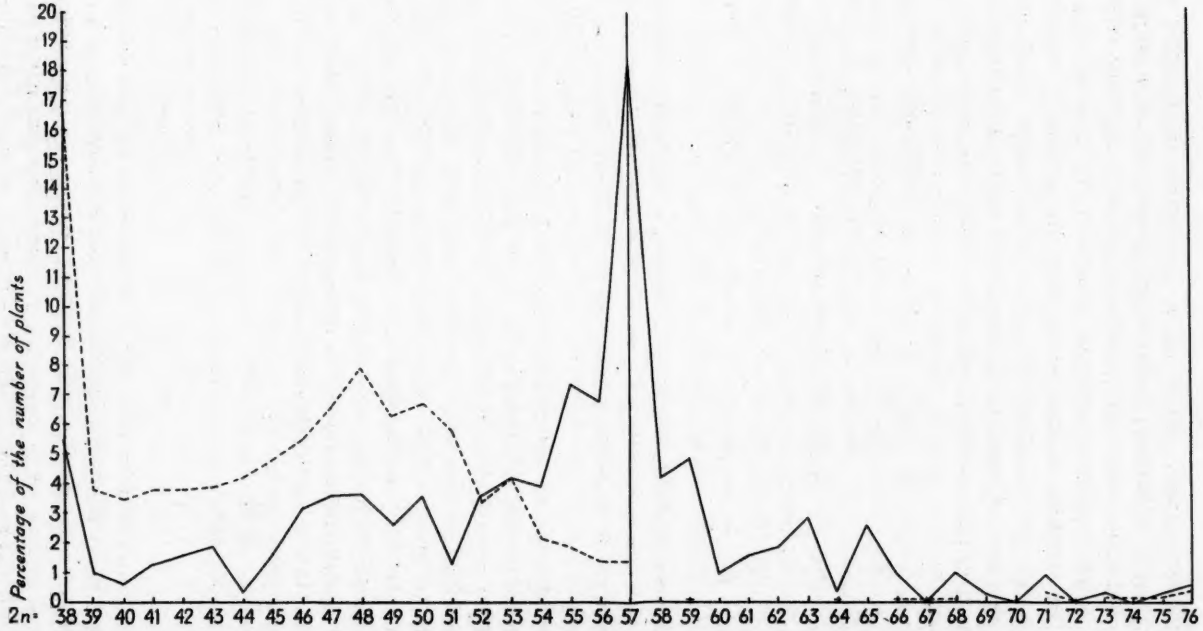

Fig. 1. Diagram showing the distribution of chromosome numbers in the progeny after the cross diploid × triploid (– – – –) and triploid × triploid *Populus tremula* (————).

present. With regard to the theoretically probable distribution, moreover, the diploid number, $2n = 38$, is enormously over-represented, like the immediately following classes. Even the tetraploid number, $n = 76$, and the immediately lower classes must be considered to be over-represented. Some suggestion of a maximum is present also in the classes midway between the diploid and the triploid numbers for $n = 45$—50. There is an under-representation, however, within the nearest classes on either side of $2n = 57$. Further, the number of individuals between 2x and 3x is considerably greater (52,1 % of the total number) than between 3x and 4x (23,3 % of the total number).

The chromosome number of the triploid progenies agrees entirely with that found in crossing triploid × diploid, the feature peculiar to the aspen that aneuploid individuals occur in a high frequency, owing to the fact that embryo-sacs and pollen-grains with aneuploid haploid numbers as well as embryos with aneuploid diploid numbers are viable.

The vitality of euploids and aneuploids. — The great majority of all individuals with aneuploid chromosome numbers possess a poor growth and have the appearance of standing on the border-line of viability. Especially weak are such plants as possess more than 57 chromosomes. Still, one comes across an occasional individual with aneuploid chromosome number that shows good growth. For the pure euploid numbers an experiment has been arranged to throw light on their relative vitality. In this experiment a diploid, a triploid and a tetraploid individual were propagated by root-cuttings. Ten 1-year-old plants of each clone were planted at random in a plot and were cut down to the surface of the ground on being planted. The diploid and triploid clones originate from wild stocks. There is therefore reason to assume that the triploid clone has arisen from a diploid via an unreduced gamete (cf. MÜNTZING, 1936). The tetraploid clone originates from an individual that had arisen in a cross between the triploid of the experiment and a diploid aspen and must therefore be indebted to an unreduced gamete in the triploid for its origin. The development during the first summer is illustrated by the following mean measurements:

	Length of stomata rel. units	Plant height cm.	Diameter of stem mm.
Diploid clone	11,08	66,6	4,60
Triploid clone	13,10	93,8	6,65
Tetraploid clone	14,40	82,2	7,10

The triploid and tetraploid clones have grown considerably faster than the diploid. However, it may be questioned whether the diploid contained in the experiment is a good representative of the average of the diploids. Probably many diploid clones occur with a better growth than the diploid of the experiment. The tetraploid clone, on the other hand, originates from the most vigorous individual of all the 34 tetraploid individuals. These 34 tetraploid individuals, 32 of which were obtained in crosses diploid × triploid, and 2 in crosses between triploid and triploid, possess a very variable vitality. The majority are very weak, and not less than 19 of the 34 died before 2 years of age. Only 3—4 give the impression of possessing full vitality. As triploids originating from diploids by restitution nuclei and thus possessing three complete genomes are apparently superior to diploids in vegetative development, it seems as if triploidy is the optimal degree of polyploidy in *P. tremula*. Tetraploidy, on the other hand, seems as a rule to be associated with weak to languishing vegetative development. Only in exceptional cases do tetraploid plants occur with good vitality. The triploid plants of the cross-progenies are, in fact, almost without exception more or less dwarfish and feeble in growth, in contrast to the triploids with gigas characters emanating from diploids by restitution nuclei. This is also readily explained by the fact that the triploids of the cross-progenies can extremely seldom possess three complete genomes, being in fact aneuploids despite the euploid chromosome number, the chromosome complement of which is characterized by sub- or supernumerariness for certain chromosome kinds, although the sum of the chromosomes is 57.

Discussion. — Of triploids in general it holds good that the chromosome numbers of their progeny do not agree with the chromosome numbers of their newly formed gametes, but, owing to a strong selection of gametes and embryos, individuals with aneuploid numbers are more or less completely absent. As a rule, the progenies both after self-fertilization and after crosses with diploids consist of diploids and individuals having one or two supernumerary chromosomes (e. g. *Datura*; BLAKESLEE and BELLING, 1934). In *Allium schoenoprasum*, LEVAN (1936) found that after self-fertilization the offspring of triploids in the great majority of cases consist of tetraploids or individuals with one or two chromosomes less than the tetraploid number. In *Populus tremula*, on the other hand, the distribution of the chromosome numbers shows a close agreement with the probable distribution of gametes with different chromosome numbers. Also here, however,

there is a distinct over-representation of individuals with the diploid number in diploid × triploid crosses as well as in triploid × triploid. On the other hand, when diploid is crossed to triploid the theoretically most numerous chromosome numbers, $\frac{38+57}{2}$, do not coincide with any euploid chromosome number. The maximum of the curve (Fig. 1), which represents the distribution of chromosome numbers in the progeny, is also less pronounced. In a cross of triploid × triploid, however, the theoretically most numerous chromosome-number class, $\frac{57+57}{2}$, coincides with the euploid number 57, and the maximum of the curve is also very marked. For the tetraploid number, too, there is a certain amount of over-representation. It is evident, therefore, that a positive selection value appears for whole multiples of the basic number 19.

Agreeing with *P. tremula* in regard to the viability of the aneuploids is *Pyrus malus*. Here, though, the chromosome numbers of the triploid progenies seem to agree entirely with the probable random distribution without any over-representation of even diploid individuals (WANSCHER, 1939). The explanation of the high frequency of aneuploids in *P. tremula* and *Pyrus malus* is probably the same, viz. that both *Populus* with $n = 19$ and *Pyrus* with $n = 17$ are secondary polyploids (JOHNSSON, 1940), an explanation that has been accepted for *Pyrus* on other grounds by DARLINGTON and MOFFET (1930).

In the cross-progeny triploid × triploid *P. tremula* plants with chromosome numbers between $2n = 38$ and 57 are far more numerous than between $2n = 57$ and $2n = 76$ (see Fig. 1). The cause of this can scarcely be an elimination of chromosomes at meiosis. In that case the maximum would have been displaced from $2n = 57$ towards $2n = 38$. Nor in all probability is the cause to be sought in an abortion of gametes with a higher chromosome number than $\frac{57}{2}$, for in a diploid × triploid cross the interval between $2n = \frac{57}{2} + 19$ and $2n = 57$ is well represented. The most probable explanation appears to be that embryos with $2n > 57$ are aborted to a great extent. The lower vitality for aneuploids with 2n between 57 and 76 than for aneuploids between 38 and 57 is in good agreement with the fact that as a rule the tetraploid plants are not very vital. It is worthy of note that no individual has been encountered with $2n > 76$. In view of the relatively high

frequency of unreduced gametes that is found among the triploids and that in crosses diploid × triploid results in 76-chromosome plants, plants with $2n > 76$ ought not to be so very rare in the progeny after crossing triploid × triploid, provided they are viable.

It would therefore seem as if the optimal degree of polyploidy in *Populus tremula* is triploidy, and that tetraploidy constitutes the limit of vitality. In agreement with this is the fact that no tetraploid species or spontaneous race is known within the genus *Populus*.

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RÖNTGENINDUZIERTE MUTATIONEN BEI PISUM SATIVUM

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(With a Summary in English)

IM Anschluss an die gross angelegten Serien zur Erforschung des Zusammenhanges zwischen Mutationen und Röntgeneffekt in der Gattung *Hordeum*, die im Genetischen Institut der Universität zu Lund von Dozent Å. GUSTAFSSON 1934 angefangen wurden, begann auch ich einige Versuche mit ähnlichem Ziel in der Gattung *Pisum*. Die Bestrahlungsexperimente wurden im Frühjahr 1935 begonnen und 1936 erweitert. Als Versuchsobjekt benutzte ich ein geeignetes Material von meinen Experimenten mit Artkreuzungen in derselben Gattung (VON ROSEN, 1942). Teils sollte untersucht werden, welche Mutationsformen bei Röntgenbehandlung auftreten können, teils sollten auch diese nachher genetisch studiert werden. Hinsichtlich der unten erwähnten dritten Linie, *Uni*, lag ein spezielles Problem vor. Diese Linie, die von LAMPRECHT (1934) beschrieben ist, wurde als eine spontane, komplexe Mutation gekennzeichnet, die sich teils in ganz sterilen pistilloiden Blüten, teils dadurch bekundet, dass die normal gefiederten Blätter zu einfachen umgebildet sind. Laut LAMPRECHT sollte dieser Typus auf Deficiency zurückzuführen sein. Ich wählte diese Linie, um die eventuelle Mutationsfrequenz in einer homozygoten Schwesterlinie zu einer spaltenden Parzelle zu prüfen.

MATERIAL UND METHODEN.

Als Ausgangsmaterial zu diesen Untersuchungen wurden ausser der oben erwähnten *Uni*-Linie noch zwei andere, nämlich *Acacia* und *de Winton* gewählt. Sämtliche Linien sind während mehreren Jahren in zusammen Zehntausenden von Individuen als Stämme vermehrt worden; vorerst von Dr. J. RASMUSSON, Hilleshög, der mir das ursprüngliche Material gütigst überlassen hat, und danach von mir. Irgendwelche spontanen Mutationen sind während diesen Jahren oder sonst während den Experimenten in den erwähnten Linien nicht beobachtet worden. Die *Acacia*-Linie besitzt folgende rezessive Gene: p_1, *m*, *le*, *r*,

tl, pl, a, fta; *de Winton*: p_1, *m, b, st, ss, wb, k, pl*; und *Uni*: p_1, *m, le, pl, a, uni.* (Bezüglich Genbezeichnung sei auf MATSUURA, 1933, verwiesen.) Die zwei ersten Linien wurden 1935, letztere 1936 bestrahlt. Die Bestrahlungen wurden im Geologischen Institut der Universität zu Lund gütigst von Dr. A. HERRLIN ausgeführt. Die Voraussetzungen und Anordnungen waren exakt dieselben, wie sie von GUSTAFSSON (1936, S. 282) angegeben worden sind (95 KV., 2,5 m. a.). Die Samen wurden in kleinen Schachteln in einer einzigen Schicht unter das Rohr gestellt. Im Jahre 1935 wurden 6 Parzellen mit etwa 65 Samen je 2, 4 und 7,2 Stunden bestrahlt, jede zweite Schachtel mit verschiedener Zeit. Von diesen zwei Schachteln wurde der Inhalt der einen 12 Stunden in kaltem Wasser bis zu kräftigem Quellen der Samen gequollen, danach leicht abgetrocknet und liegen gelassen, sodass die Keimung 2 bis 3 Stunden vor der Bestrahlung begann. Die Serie 1936 (*Uni*-Linie) umfasste 200 Samen von je 12 Gruppen, von denen die Hälfte sofort nach der Bestrahlung gesät wurde und der Rest zehn Tage später. In jeder Gruppe wurden zwei Proben 4, 5 bzw. 6 Stunden bestrahlt. (Wegen verschiedenen Lagen zur Antikathode entsprechen die wahren Bestrahlungsintensitäten 4 Stunden für zwei Proben, 5 St. für 4, 6 St. für 4 und 9 Stunden für zwei Proben.) Die Hälfte der Gruppen jeder Bestrahlungszeit wurde auf folgender Weise gequollen: $5\,^1/_2$ Stunden Quellung in kaltem Wasser, leichtes Abtrocknen und danach Vorkeimung $1\,^1/_2$ Tage ehe sie bestrahlt wurden. Leider wurde der Röntgeneffekt während der Bestrahlung nicht mit der Jonisationskammer gemessen. Es kann jedoch behauptet werden, dass weder die Strahlen besonders hart noch die Dosen besonders hoch gewesen sind. Diese Vermutung gewinnt noch an Wahrscheinlichkeit durch die Mitteilung von ATABEKOWA (1936), nach der die Erbsen gegen Röntgenstrahlen empfindlich sind. Sämtliche untersuchten Generationen wurden im Freien gesät. Von den Generationen X und X_1 sind alle erhaltenen Samen und Familien ausgesät worden, im allgemeinen nicht weniger als 25 Samen je Parzelle, von X_2, X_3 und X_4 aber nur mit wenigen Ausnahmen diejenigen Familien, die mehr als 30 Samen gehabt haben.

Die statistische Bearbeitung ist nach BONNIER und TEDIN (1940) durchgeführt worden. Für die Wahrscheinlichkeitsberechnungen sind folgende Bezeichnungen benutzt: bei χ^2-Analysen gibt $- = P > 0{,}05$, $* = P\ 0{,}05 — 0{,}02$, $*^+ = P\ 0{,}02 — 0{,}01$, $** = P\ 0{,}01 — 0{,}001$, $*** = P < 0{,}001$ und $**** = P$ erheblich $< 0{,}001$ an. Für die Varianzquoten gibt $- = P\ 0{,}02$, $* = P\ 0{,}05$, $** = P\ 0{,}01$ und $*** = P\ 0{,}001$ an.

Aus dem Folgenden geht hervor, dass individuelle Mutationen ver-

einigt worden sind, wenn die χ^2-Analyse der Spaltungszahlen eine signifikative Heterogenität zwischen den Parzellen der X- und X_1-Generationen anzudeuten schien. Eine Signifikanz zwischen den Parzellen von X_2 und X_3 scheint dafür zu sprechen, dass in den einzelnen Mutationen eine gewisse Selektion stattgefunden hat (z. B. eine Fertilitätsdifferenzierung).

DER ALLGEMEINE RÖNTGENEFFEKT.

Unter »allgemeinem Röntgeneffekt» verstehe ich den Einfluss der Bestrahlung, der sich in der X-Generation (d. h. die bestrahlten Samen) beobachten lässt, wie vegetative Entwicklung der Pflanzen, Keimung, Ernte u. s. w.

Die Acacia-Serie. — Diese Serie zeigte, dass die Pflanzen in der X-Generation von denen der Normallinie nur dadurch abwichen, dass sie in den Parzellen, die 7,2 Stunden bestrahlt wurden, im Durchschnitt ein wenig kleiner waren als in den übrigen Parzellen. Da die Anzahl der Parzellen in dieser Serie zu gering ist um eine statistische Bearbeitung zu erlauben, können nur die Mittelwerte zahlenmässig verglichen werden. Wenn zuerst die verschiedenen Bestrahlungszeiten, die wie oben erwähnt 2, 4 und 7,2 Stunden betrugen, berücksichtigt werden, so geht hervor, dass die Keimungsmittelwerte je Parzelle den r-Dosen im grossen umgekehrt proportional sind: 85,5 %, 45,5 % bzw. 46,0 %. Die Anzahl der Hülsen je Pflanze (jede Pflanze wurde einzeln geerntet und mit der Hand gedroschen, wobei die Anzahl Hülsen und die Gesamtzahl Samen ermittelt worden sind) war 6,24, 6,89 bzw. 6,15 und die Anzahl Samen je Hülse (mit Hilfe der oben erwähnten Zahlen berechnet) 2,81, 2,60 bzw. 2,44. Das Prozent blühender Pflanzen für die ganze Parzelle, so berechnet, dass als blühende Pflanzen alle Individuen gezählt wurden, die ihre erste Blüte ganz offen halten, betrug am 25. VI. (= 55 Tage nach der Saat) 66,5, 37,5 bzw. 31,0 %. Bei sämtlichen Bestrahlungszeiten sind eine oder wenige Röntgenmutationen aufgetreten. Eine unbehandelte Schwesterlinie, die unter genau denselben Bedingungen neben den Bestrahlungsparzellen kultiviert worden ist, zeigte 73,0 % Keimung, 5,15 Hülsen je Pflanze, 3,35 Samen je Hülse und am 25. VI. 75,0 % blühende Pflanzen. Aus dem oben Angeführten dürfte hervorgehen, dass die Anzahl Samen je Hülse, die als ein Charakteristikum für die Fertilität der Pflanze aufzufassen ist, umgekehrt proportional ist der Steigerung der Bestrahlungsdosis. So verhält es sich auch mit der Anzahl blühender Pflanzen, d. h. je länger die Bestrahlung, je schwächer die Entwick-

lung. Was die Anzahl Hülsen je Pflanze und die Keimung betrifft, so ist wahrscheinlich irgend eine äussere Störung dazugekommen, die diese kleine Versuchsserie verrückt hat. Bei einem Vergleich mit den Daten für die Normallinie geht hervor, dass die kleinste Bestrahlungszeit zu gross ist, um eine stimulierende Einwirkung haben zu können. Eine solche Beobachtung wird aber von ATABEKOWA (1936), KRAJEVOJ (1935) und VILLERTS (1937) erwähnt.

Wenn man die Nachkommen der trockenen und der gequollenen Samen der X-Generation vergleicht, so zeigt sich, dass die gequollenen Parzellen besser sind. Die Keimung betrug 56,2 bzw. 61,8 %. Die Anzahl Hülsen je Pflanze war 5,10 bzw. 7,77; die Anzahl Samen je Hülse 2,35 bzw. 2,87; und das Prozent blühender Pflanzen 38,3 bzw. 52,0. 25 % der gekeimten Pflanzen der X-Parzellen waren wegen *Fusarium*, Dürre oder verspäteter Entwicklung unterlegen. In unbehandelten Parzellen war der entsprechende Verlust 1 %. Eine Variationsanalyse der *Anzahl Hülsen je Pflanze* zeigt ein mittleres Quadrat für den Vergleich *zwischen* Parzellen (= Röntgeneffekt) von 36,8 mit 5 Freiheitsgraden. Das mittlere Quadrat für den Vergleich *innerhalb* der Parzellen (Fehler) ist 12,3 mit 131 D.F. Der Quotient *zwischen/innerhalb* beträgt 2,99*. Die durchschnittliche Anzahl Hülsen je Pflanze ist $6{,}43 \pm 0{,}098$ für die bestrahlten und $5{,}15 \pm 0{,}22$ für die unbehandelten. Diff./m = 5,9. Die *Anzahl Samen je Hülse* zeigt für *zwischen* Parzellen 0,4, D.F. = 5, und für *innerhalb* Parzellen 0,7 mit D.F. 131. Der Quotient *zwischen/innerhalb* beträgt $0{,}6^-$. Die durchschnittliche Anzahl Samen je Hülse ist $2{,}62 \pm 0{,}073$ für behandelte und $3{,}35 \pm 0{,}076$ für unbehandelte. Diff./m = 7,0.

Zusammenfassend ist also zu sagen, dass die *Acacia*-Linie im ganzen so reagiert, wie zu erwarten war, und in gleicher Weise, wie dies GUSTAFSSON (1940) für die Gerste gezeigt hat. Es sei jedoch hervorgehoben, dass der Sterilitätseffekt sehr unsicher ist.

Die de Winton-Serie. — Bemerkenswert ist, dass hier trotz gleichen Bestrahlungszeiten keine einzige Mutation angetroffen worden ist. Dagegen zeigten die X-Pflanzen einen deutlichen physiologischen Effekt der Bestrahlung. Besonders in den gequollenen Parzellen traten einige kleine, verzwergte, »struppige» Pflanzen auf. Es sei erwähnt, dass der *de Winton*-Typus durchschnittlich 1,5 m hoch ist, während die am stärksten bestrahlten Pflanzen nur 15—30 cm Höhe erreichten. In den übrigen Parzellen gab es alle sonstigen Übergänge. Sogar sämtliche Pflanzen der bestrahlten Parzellen zeigten eine Anthozyanfärbung der Stengel, und einige waren extrem stark gefärbt. KRAJEVOJ (1935)

und VILLERTS (1937) berichten über eine ähnliche Erscheinung, machen aber keine Angaben über die Pflanzengrösse.

Bei einem Vergleich zwischen dem Einfluss der Bestrahlungszeiten ergibt sich folgendes: Die Keimung beträgt für 2 Stunden Bestrahlung 72,5 %, für 4 Stunden 51,0 % und für 6 Stunden 46,5 %. Die Anzahl Hülsen je Pflanze ist 5,71, 5,46 bzw. 5,65; die Anzahl Samen je Hülse: 3,79, 3,48 bzw. 3,70 und die entsprechenden Zahlen für das Prozent blühender Pflanzen sind für den 2. VII. (62 Tage nach der Saat) 75, 62 bzw. 42 %. Für die unbehandelte Schwesterlinie sind die entsprechenden Daten: 94,0 %, 6,64 Hülsen, 3,88 Samen und 75 % Blüten. Der Zusammenhang zwischen Bestrahlungszeiten und Pflanzenreaktion ist hier ungefähr derselbe wie in der vorigen Serie, nur mit dem Unterschied, dass die höchste Bestrahlungszeit, die 6 Stunden beträgt, in der *Acacia*-Serie 7,2 Stunden, hier nicht so stark von den übrigen Zeiten abweicht. Der Unterschied zwischen trockenen und gequollenen Samen geht in dieser Serie in die andere Richtung: 79,0 bzw. 34,0 % Keimung, 6,30 bzw. 4,91 Hülsen, 3,57 bzw. 3,74 Samen und 70 bzw. 47 % blühende Pflanzen. Die Variationsanalyse der *Anzahl Hülsen je Pflanze* gibt keinen statistischen Ausschlag: Das mittlere Quadrat für *zwischen* Parzellen ist 10,40 mit D.F. = 5, und für *innerhalb* Parzellen 5,41 mit D.F. = 74. Der Quotient *zwischen/innerhalb* beträgt $1{,}92^{-}$. Die durchschnittliche Anzahl Hülsen je Pflanze ist $5{,}60 \pm 0{,}27$ für bestrahlte und $6{,}64 \pm 0{,}42$ für unbestrahlte Parzellen. Diff./m = 2,1. Die *Anzahl Samen je Hülse* gibt für *zwischen* Parzellen ein mittleres Quadrat von 0,60 mit D.F. = 5 und für *innerhalb* Parzellen 1,05 mit D.F. = 74. Der Quotient, der $0{,}6^{-}$ ist, gibt also an, dass die Bestrahlung von *de Winton* keine nachweisbare Sterilität hervorgerufen hat. Die Durchschnittswerte für Samen/Hülse sind $3{,}66 \pm 0{,}11$ bzw. $3{,}88 \pm 0{,}12$. Diff./m = 1,4.

Zusammenfassend kann also gesagt werden, dass *de Winton* sich im ganzen unempfindlich gegen Röntgenstrahlen zeigt. Da sowohl *Acacia* wie *Uni* (siehe unten) sich empfindlicher gezeigt haben und beide niedrige, weissblütige Typen sind, während *de Winton* hoch und rotblütig ist, so läge es nahe anzunehmen, dass die Ursache in einer genetischen oder morphologischen Verschiedenheit zu suchen wäre. Gegen diese Annahme spricht aber folgendes: RASMUSSON (1938) weist zwei Mutationen in einem sehr schwach bestrahlten, hohen, weissen Typus nach. (Er bestrahlte nur 42 Minuten unter ungefähr denselben Verhältnissen wie ich.)

Die Uni-Serie. — Im Vergleich mit den oben erwähnten Serien traten in dieser reichlich Chlorophyllmutationen auf. Irgend eine

andere morphologische Form war nicht nachzuweisen. Tabelle 1 vergleicht verschiedene Behandlungen und Beurteilungen. (Wegen Platzmangel konnten die 4 Stunden bestrahlten Parzellen nur in der X-Generation geprüft werden.) Die Blühte ist hier durch die Anzahl Tage angegeben, die von der Saat bis zu dem Tag verfloss, wo 75 % sämtlicher Pflanzen der Parzelle ihre erste Blüte geöffnet hatten. Der Zusammenhang mit den Bestrahlungszeiten ist für Keimung und Blühte am wenigsten ausgeprägt, dagegen scheint eine sehr deutliche

TABELLE 1. *Allgemeine Beeinflussung der X-Parzellen. Durchschnittswerte der Uni-Serie.*

Behandlung	% Keimung	Anzahl Hülsen je Pflanze	Anzahl Samen je Hülse	Anzahl Tage bis 75 % Blühte	% Mutanten
Unbehandelt	53,7	20,5	4,530	59,0	—
Röntgen					
4 Stunden	51,0	19,3	4,017	66,0	Unbekannt
5 »	53,0	18,6	3,852	66,5	17,7
6 »	52,0	14,3	3,568	70,5	4,5
9 »	13,0	11,8	3,204	68,5	7,5
Metabolismus					
Trockene Samen	46,6	14,1	3,695	67,8	71,0
Gequollene »	44,7	18,2	3,692	66,8	29,0
Vorkeimung					
Späte Saat	56,8	15,4	3,596	69,8	52,0
Frühe »	34,9	16,9	3,784	65,9	48,0

Korrelation sowohl mit der Anzahl Hülsen je Pflanze als mit der Anzahl Samen je Hülse zu bestehen. Der Unterschied zwischen trockenen und gequollenen Samen ist sehr schwankend und unsicher. Die frühe, d. h. die Saat unmittelbar nach der Bestrahlung, scheint am günstigsten gewesen zu sein, was indessen, um recht verstanden zu werden, in Zusammenhang mit den Witterungsverhältnissen gebracht werden muss. Jedenfalls geht hervor, dass die Ruheperiode keine grössere Anzahl gestörter Zellen zur Folge gehabt hat. Von den X-Pflanzen sind 26 % zwischen Keimung und Ernte eingegangen, während diese Zahl für die Linie nur 13 % erreicht hat. Die Variationsanalyse der *Anzahl Hülsen je Pflanze* für *zwischen* Parzellen ergibt ein mittleres Quadrat von 1452,2 mit D.F. = 11, und für *innerhalb* Parzellen 102,4 mit D.F. = 1087. Der Quotient ist $14{,}2^{***}$. Die durchschnittliche

Anzahl Hülsen je Pflanze beträgt $16{,}44 \pm 0{,}32$ für behandelte und $20{,}46 \pm 1{,}51$ für unbehandelte Parzellen. Diff./m = 2,6. Für die *Anzahl Samen je Hülse* sind die entsprechenden Werte 22,8 mit D.F. = 11 und 0,75 mit D.F. = 1087, was einen Quotienten von 30,4*** ergibt. Die durchschnittliche Anzahl Samen je Hülse ist $3{,}75 \pm 0{,}03$ bzw. $4{,}53 \pm 0{,}073$ mit Diff./m = 9,9.

Die *Uni*-Serie zeigte sich also im allgemeinen ziemlich empfindlich gegen X-Strahlen, obgleich die Wirkung nach allen Ergebnissen zu urteilen nicht ganz proportional zu sein scheint. Schön sind aber die Zahlen für die Anzahl Hülsen je Pflanze und Samen je Hülse (partielle Sterilität).

Zusammenfassend ist festzustellen, dass der Einfluss der Bestrahlung auf die X-Generation (die Pflanzen, die sich unmittelbar aus den bestrahlten Samen entwickeln) in der Gattung *Pisum* so zutagetritt, wie dies vor allem auf Grund den Untersuchungen von GUSTAFSSON (1938, 1940, 1941) bei *Hordeum*, STADLER bei *Zea*, STUBBE bei *Antirrhinum* und MULLER und anderen bei *Drosophila* zu erwarten war.

DIE MUTATIONSTYPEN.

Sämtliche 22 Mutationen, die in diesen Bestrahlungsserien angetroffen worden sind, sind einfach rezessiv, mehr oder weniger letal. Alle beziehen sich auf Chlorophylleigenschaften. Keine einzige Mutante, die eine andere, vegetative Eigenschaft betrifft, wurde beobachtet. Allerdings habe ich mehrere vermutet, aber sie haben sich sämtlich als rein modifikativ erwiesen. Über einen Fall von trichterförmigen Blättern mit sterilen Blüten, mithin eine Komplexmutation, die nach X-Strahlenbehandlung aufgetreten ist, berichtet indessen RASMUSSON (1938).

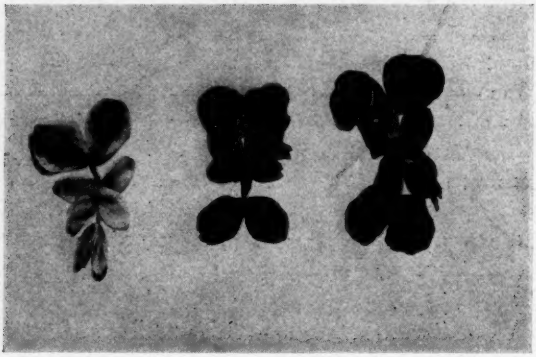
Von den 22 Mutationen zeigen mehrere denselben Phänotypus, weshalb diese in dieselbe Gruppe eingereiht worden sind. Einige von diesen sind nur in X_1 als einige einzelne Pflanzen beobachtet und genau bestimmt worden. Da sie in den direkten Nachkommenschaften nicht mehr aufgetreten sind, konnten sie jedoch nicht studiert werden. Unten folgt eine Beschreibung der Morphologie und Genetik der 7 verschiedenen Phänotypen.

DIE ACACIA-SERIE.

Die Mutante chr—w (Albo-viridis Chimären-Typus). — Die *Acacia*-Serie gab zwei Chlorophylltypen, von denen *chr—w* der eine ist (Fig. 1). Er wird so genannt, weil die Grundfarbe weiss ist. Die weisse Farbe ist besonders interessant, da es, wie später gezeigt wird, eine Eigenart

für *Pisum* im Vergleich mit anderen Pflanzengattungen ist, äusserst wenige *Albina*-Formen zu liefern. *chr—w* ist indessen kein gewöhnlicher *Albina*-Typus, sondern eine genetisch bedingte Chimäre vom Sektorialtypus. Nach CORRENS (siehe DE HAAN, 1933) sollte er »*albo-marginata* Typus» genannt werden. FRUWIRTH beschrieb 1920 einen ähnlichen spontanen Typus und nach DE HAAN soll SPRENGER 1916 etwas Ähnliches gefunden haben.

Die Mutante trat zum erstenmal mit einer einzigen Pflanze in einer X_1-Parzelle auf (611/1936). Die Chlorophyllpflanzen erschienen hell weissgelb mit grünen Mittelnerven und grünem Stamm (Fig. 1 *c*). Die



c *b* *a*

Fig. 1. *Acacia*-Serie: *a*) Normale Pflanze, *b*) *chr—y* und *c*) *chr—w*. Die Blätter sind von ungefähr eine Woche alten Pflanzen.

Ränder der Blättchen des zweiten Blattes sind beinahe ganz weiss, während die Nerven und grössere oder kleinere Partien (Flecken) dunkelgrün sind. Gewisse Pflanzen sterben in diesem Stadium ab. 50—75 % verbleiben aber am Leben und bekommen allmählich noch grössere grüne Partien, während ein Zweigsektor oder eine ganze Seite der Pflanze ganz weiss verbleibt. Diese Pflanzen blühen ungefähr zur selben Zeit wie die Linie, sind aber nur $^1/_4$ so gross (Fig. 2). Im allgemeinen pflegt nur eine Hülse mit 1—3 guten Samen ausgebildet zu werden. Eine Hülse mit Samen von einer *Albina*-Partie wurde bisher jedoch nicht erhalten. Die Chlorophyllpflanzen verwelken schneller als die Normallinie. Nachkommen von solchen homozygoten Rezessiven sind untersucht worden. Im Jahre 1939 gaben im Gewächshaus von 15 Parzellen (jede einer bestimmten cx-Pflanze entsprechend) zwei 5 grüne : 3 rezessive Pflanzen. Die übrigen waren ganz normal und grün.

Die Keimung war 87 % in den spaltenden und 66 % in den homozygot grünen Parzellen. Von den im Jahre 1941 am freien Feld geprüften 11 ähnlichen Parzellen zeigte keine Spaltung. Alle waren auch hier normal grün (Keimung 46 %). Zu beiden diesen Kontrollen ist jedoch zu bemerken, dass die Samenanzahl je Parzelle nur ungefähr 1—5 betragen hat. Der grösste Teil der Hülsen stammte aus ganz grünen Partien der Mutterpflanze. Es scheint somit, als ob die vermeintlichen homozygot Rezessiven die Entstehung verschiedener Pflanzen veranlassen könnten. Die Erscheinung ist jedoch wahrscheinlich so zu verstehen, dass ganz grüne Partien nur grüne Nachkommen geben, Hülsen der Chimärenpartie spaltende Nachkommenschaften und ganz weisse

Fig. 2. *Acacia*-Serie: Blühende Normalpflanze (rechts) und *chr—w* (links).

Partien nur Chlorophylltypen geben. Die letzte Möglichkeit konnte leider nicht geprüft werden. Der Typus hat eine gewisse Ähnlichkeit mit den von KAJANUS (1919) beschriebenen *Xantha-variegata*-Formen. Diese waren indessen gelb gefleckt, was möglicherweise die Ursache dafür gewesen ist, dass KAJANUS von seinen rezessiven Pflanzen meistens bunte Nachkommen bekam. Mein Typus ist jedoch der gelben *Variegata*-Form von FRUWIRTH (1920) noch ähnlicher, die offenbar genau dasselbe Spaltungsbild gezeigt hat.

Wie schon erwähnt, erscheint dieser Chimärentypus genotypisch bedingt. Die Spaltungen sind fünf Generationen hindurch geprüft worden, wobei insgesamt $0{,}895 \pm 0{,}057$ Rez. je 4 Individuen resultierten (887 Pflanzen). Diff./m = 1,84. Die Spaltungen in X_1 und X_2 waren schön mit Diff./m = 0,26 und 0,52, während X_3 zu viele Rezessive zeigte: $1{,}155 \pm 0{,}16$ je 4; Diff./m = 0,97. X_4 zeigte die schlechteste Spaltung mit Diff./m = 2,34 (753 Pflanzen). Die Anzahl nicht spaltender Parzellen war ein wenig zu hoch; für X_2—X_4 von 1,04—1,80 je 3. Die in dieser

Hinsicht mit der Erwartung am besten übereinstimmende Generation war X_4. Die Keimung zeigte für die spaltenden Parzellen einen besseren Wert: X_3 keimte 74 % in den spaltenden und 68 % in den nicht spaltenden; 64 und 40 % waren die entsprechenden Werte für X_4. Keine der Generationen zeigte zwischen den Parzellen eine signifikative Heterogenität in den Spaltungszahlen *zwischen* spaltenden Generationen oder *innerhalb* derselben (berechnet nach der χ^2-Methode).

Aus dem oben Angeführten geht hervor, dass der Chlorophylltypus durch ein einfaches, rezessives Gen bedingt wird. Die Nachkommen der rezessiven Pflanzen verhielten sich aber so, dass man auch an sekundäre Einflüsse denken muss (z. B. durch modifikative Gene).

Die Mutante chr—y (Lutescens-Typus). — Diese Mutante ist auch in der *Acacia*-Serie aufgetreten (Fig. 1 *b*), und zwar gleichzeitig mit zwei verschiedenen Pflanzen der X-Generation: 528/1936 und 603/1936. Die Mutante wird am besten als *Lutescens*-Typus nach GUSTAFSSON klassifiziert. Sie erscheint hellgrün bis tauig *Chlorina*-grün, häufig so dunkel, dass sie sich im ersten Stadium schwer von normalen Pflanzen unterscheiden lässt. Nach einigen Tagen bekommt sie eine hellgrüne Farbe, die in Gelb übergeht. Nach dem Ausbilden von 2 bis 3 Paar Blättern (= 10—14 Tage nach der Keimung) verwelkt diese Mutante. Dieser Typus wird durch ein einfaches rezessives Gen bedingt. 1361 Pflanzen während 4 Generationen gaben $0{,}_{681} \pm 0{,}_{047}$ Rez. je 4 mit Diff./m = $6{,}_8$. Nur X_4 zeigt ein ähnliches Rezessivendefizit. Studiert man das Verhältnis zwischen spaltenden und nicht spaltenden Parzellen, so ergibt sich, dass die Anzahl nicht spaltender Parzellen in X_3 und X_4 zu gross ist ($1{,}_{200}$—$1{,}_{560}$ pro 3); X_1 und X_2 geben mit ihren kleinen Zahlen noch schlechtere Werte. Die Keimung ist für spaltende Parzellen eher besser als für homozygot grüne Parzellen (49 spaltende mit durchschnittlich 79 % und 53 nicht spaltende Parzellen mit 50 % Keimung in X_4). Nach einer χ^2-Analyse der Spaltungen zeigt sich die Abweichung der *Totalspaltung* als dominierend: $45{,}_{91}$*** mit D.F. = 1. Für *zwischen* Generationen (Jahrgänge) ergibt sich ein χ^2 von $9{,}_{46}$*;+ mit D.F. = 3. Nur die Heterogenität *zwischen* Parzellen in X_1 zeigt einen Ausschlag, nämlich $3{,}_{67}$* mit D.F. = 1. Aber die Anzahl der Glieder war zu gering, um einen Zusammenhang beweisen zu können.

DIE DE WINTON-SERIE.

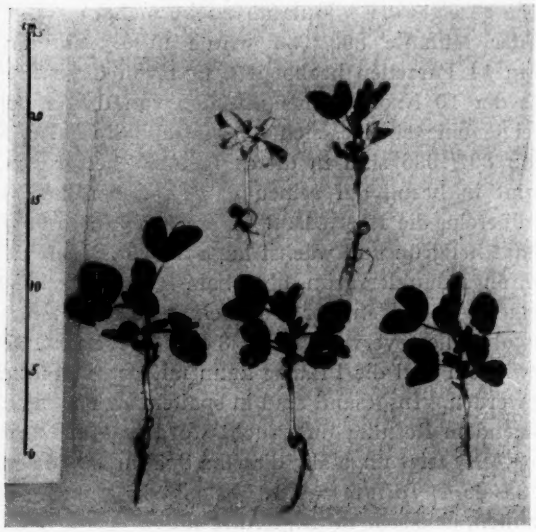
Wie schon oben erwähnt, fand ich in der *de Winton*-Serie überhaupt keine Mutationen. Sämtliche Chlorophyllmutanten, die unten beschrieben werden, stammen somit aus der *Uni*-Serie, die teils die

grösste Versuchsserie bildete, teils auch prozentuell die meisten Mutationen gegeben hat.

DIE UNI-SERIE.

Die Mutante chr—d (*Xantha-Typus*). — Diese Mutante hat exakt dieselbe Morphologie wie die von RASMUSSON (1938) mit demselben Namen belegte. Sie ist also gelblich weiss und lebt nur so lange als die Speichernahrung reicht und bildet keine Spur von Chlorophyll aus (Fig. 3 *d*). Sie wird nur 2—4 cm hoch und stirbt nach 1 bis 2 Wochen

d *e*



a *b* *c*

Fig. 3. *Uni*-Serie: *a*) Normalpflanze, *b*) *chr—l* oder *chr—o*, *c*) *chr—a*, *d*) *chr—d* und *e*) *chr—g*. Eine bis zwei Wochen alte Pflanzen.

oder früher. Die Mutante erschien viermal in drei verschiedenen X-Parzellen. Die Gesamtspaltung zeigte ein sehr grosses Rezessivendefizit: $0{,}392 \pm 0{,}066$ je 4 mit 686 Individuen. Diff./m = 9,2. (Bei 15 : 1-Spaltung wäre Diff./m = 3,7). Sämtliche Generationen zeigen ein Defizit entsprechender Grösse. Die Anzahl nicht spaltender Parzellen ist viel zu gross, nämlich 2,51 in X_2 und 2,17 in X_3. (Bei 15 : 1-Spaltung wäre der entsprechende Wert 1,4). Es ist aber zu bemerken, dass die Anzahl Parzellen in keiner Generation mehr als 40 erreichte. Die Keimung in spaltenden und homozygoten Parzellen ist nicht verschieden, sondern beträgt in beiden etwa 78 %. χ^2 der *Totalspaltung* = $84{,}90^{***}$,

D.F. = 1, während die Heterogenität weder *zwischen* noch *innerhalb* der Generationen irgend eine Signifikanz zeigt. Nach dem Verhalten der Anzahl nicht spaltender Parzellen ist anzunehmen, dass auch diese Mutante einfach rezessiv ist. Das Rezessivendefizit ist wahrscheinlich auf eine Gametenelimination zurückzuführen (siehe S. 336).

Die Mutante chr—a (*Lutescens-Typus*). — Die Mutante *chr—a* ist in drei verschiedenen X-Parzellen mit zusammen 6 Individuen aufgetreten, von denen drei weiter studiert werden konnten; sie gehören alle zu derselben ursprünglichen X-Parzelle. Es hat sich überhaupt als schwierig gezeigt, diese Mutante zu vermehren. Die Nachkommenschaft der Mutante 802/1936 wurde in X_2 nur an ein Paar Individuen in 14 Parzellen beobachtet, und von diesen spalteten nur drei. Keine der 10 Nachkommenparzellen von diesen heterozygoten Pflanzen zeigte eine einzige, sichere Chlorophyllpflanze. Die Nachkommen von 807/1936 sind in dieser Hinsicht besser gewesen. Der Typus stimmt in bezug auf seinen ganzen Lebenslauf mit der Beschreibung überein, die RASMUSSON (1938) für seinen *ch—a* mitgeteilt hat. Er keimt hellgrün und wächst langsam. Die Mitte der Blättchen erscheint anfangs dunkler grün, aber bald bekommen die Ränder der Blättchen einen gelben Ton, der sich mehr und mehr über die Pflanze verbreitet, wobei diese verwelkt (Fig. 3 *c*). Vier Paar Blätter pflegen sich zu entwickeln und die Pflanze kann mit verkümmerten Schossen 1 dm hoch werden. Insgesamt sind in spaltenden Parzellen 391 Pflanzen mit folgendem Resultat untersucht worden: $0{,}561 \pm 0{,}087$ Rez. je 4. Diff./m = 5,0. X_3 zeigt ungefähr dieselbe Spaltung, während X_2 besser ist ($0{,}700 \pm 0{,}16$ je 4; Diff./m = 1,9). X_1 gibt hier, wie sonst bei allen diesen Mutanten, eine sehr niedrige Anzahl Rez.: $0{,}276 \pm 0{,}23$. Die Anzahl nicht spaltender Parzellen ist auch zu hoch: $X_2 = 2{,}50$ und $X_3 = 2{,}15$ mit im ersten Fall 40 und im letzteren 25 Parzellen. Im Gegensatz zu dem Verhalten bei der Spaltung ist also hier X_2 die schlechtere Generation. Die Keimung ist in beiden Typen von Parzellen dieselbe. Es ist indessen zu bemerken, dass die Keimung 1939 für die Nachkommenschaft in X_2 von 802/1936 nur 37 % bzw. 33 % betrug, während die von 807/1936 76 % bzw. 46 % erreichte. Im nächsten Jahr in X_3 haben indessen diese beiden Serien eine Keimung von 80 % erreicht. Die *Totalspaltung* ergibt eine χ^2 von $24{,}93^{***}$ mit D.F. = 1. Eine Heterogenität in der einzelnen studierten Linie ist kaum zu beobachten. Eine Variationsanalyse der Anzahl *Samen/Hülsen* in X_2 gibt (vgl. S. 330) einen Quotienten von $3{,}83^{**}$ für *zwischen* und *innerhalb* den Parzellen (das mittlere Quadrat ist im ersten Fall = 3,60 mit D.F. = 6 und

im zweiten = 0,94 mit D.F. = 45), was anzudeuten scheint, dass innerhalb dieses Mutationstypus verschiedene Fertilitätslinien auftreten. Bemerkenswert ist auch, dass das morphologische Bild dieser Mutante nicht so stabil ist, wie dies mit den meisten anderen der Fall ist.

Die morphologische Gruppe *chr—a* scheint mehrere wesentlich verschiedene genetische Einheiten (Aberrations-Typen?) zu enthalten.

Die Mutante chr—l (*Virescens-Typus*?). — Diese Mutante stimmt mit RASMUSSONS *chl* überein. Sie entwickelt sich hellgrün. (*chl* ist indessen in ihrem ersten Stadium schwer von normalen Pflanzen zu unterscheiden.) *chr—l* ist während der ersten Woche gegen Dürre sehr empfindlich, wobei sie ungefähr wie *chr—a* gelb wird und eingeht. Unter günstigen Verhältnissen wächst die Chlorophyllpflanze langsam, was *chr—a* selten tut, und wird immer grüner bis sie eine etwa normalgrüne Farbe angenommen hat (Fig. 3 *b*). Gewisse Pflanzen gelangen zur Blühte und setzen einzelne Hülsen mit ein oder ein Paar Samen an, die doch kaum keimfähig sind. Die Chlorophyllpflanze erreicht niemals mehr als $^1/_4$ der Grösse des Normaltypus. Die Mutante trat in zusammen drei Parzellen fünfmal auf. Die Gesamtspaltung war 0,762 ± 0,037 Rez. je 4 mit 2219 Individuen (Diff./m = 6,4) und die verschiedenen Generationen zeigten ungefähr dasselbe Rezessivendefizit. Das Verhalten spaltender zu nicht spaltender Parzellen zeigte auch hier dieselben Eigentümlichkeiten wie bei *chr—a*. So beträgt der Durchschnitt für sämtliche Generationen der nicht spaltenden Parzellen von 802/1936 2,72, von 804/1936 2,07 und von 807/1936 1,90. Aber die zwei letztgenannten Linien zeigen in X_3 ein viel besseres Verhalten als die erstere. 0,71 bzw. 0,97 gegenüber 2,34 je 3. Die Keimung war auch hier 1939 niedrig (etwa 55 %), aber 1941 (X_3) erreichte sie 80 %. Zwischen den Parzellentypen besteht kein nachweisbarer Unterschied.

Die χ^2-Analyse der Spaltungen ergibt folgende Zusammenstellung:

		D.F.
$\Sigma\ \chi^2$ der summierten Spaltungszahlen	= 42,35***	1
Het. *zwischen* Parz. in X_3 oder zw. Pfl. *innerhalb* d. Parz. X_2	= 36,41 —	32
» » » » X_2 » » » » » X_1	= 55,09***	14
» » » » X_1 » » » » » X	= 2,73 —	4
» » » » X	= 25,59***	6
» » Generationen	= 13,65***	2
$\Sigma\Sigma\ \chi^2$	= 175,82***	59

Eine Variationsanalyse von *Samen je Hülse* in X_2 ergibt den Quotienten 3,35** für das Verhalten *zwischen* und *innerhalb* der Parzellen (M-Quadrat = 4,21, D.F. = 9 bzw. 1,26, D.F. = 123). Auf Grund dieser Zahlen ist zu vermuten, dass diese morphologische Gruppe aus mehre-

ren genetisch oder zytogenetisch verschiedenen Mutanten zusammengesetzt ist. Dass auch physiologische oder klimatologische Faktoren einen Einfluss haben, zeigt die variierende Heterogenität zwischen den Generationen (Jahrgängen), was ferner die oben erwähnte Beobachtung über die Empfindlichkeit des Typus gegen die Witterung bestätigt.

Die Mutante chr—o (Chlorina-Typus). — Die Mutante *chr—o* ist am nächsten mit einem *Chlorina*-Typus zu vergleichen, wie er von GUSTAFSSON (1940) definiert wird oder wie ihn RASMUSSON (1938) für *Pisum* beschreibt. Ein wesentlicher Unterschied liegt aber vor: es ist nämlich beinahe unmöglich homozygote, rezessive Linien zu erhalten. Nicht nur in dieser Hinsicht gleicht sie sehr *chr—l*. *chr—o* entwickelt sich hellgrün (»*Chlorina*-grün») und wächst anfangs gut, bis sie eine fast normalgrüne Farbe bekommt. Das Wachstum hört bei einer Grösse von 2—3 dm auf, wenn die Pflanze etwa $^1/_3$ der Grösse des Normaltypus erreicht hat. Mehrere der Chlorophyllpflanzen sterben in diesem Stadium, wobei sie verwelken, ohne einen gelben Farbenton zu zeigen. Andere Chlorophyllpflanzen aber gelangen zur Blühte und entwickeln einzelne Hülsen mit einigen Samen. Diese Samen geben konstant rezessive Nachkommen. Die Gesamtspaltung war $0{,}842 \pm 0{,}032$ Rez. je 4 mit 2973 Individuen. Diff./m = 4,9. X_2 zeigte beinahe dieselben Spaltungsverhältnisse, während X_3 etwas besser war. Dieser Typus erschien 7 Mal in vier verschiedenen X-Parzellen. Drei von diesen Linien konnten studiert werden; sie zeigten alle dasselbe morphologische Bild. Dagegen verhielt sich die Anzahl spaltender zu nicht spaltender Parzellen in der Weise wie bei *chr—l*. D. h. die durchschnittliche Anzahl nicht spaltender Parzellen für sämtliche Generationen berechnet je 3 für die drei Linien ist: 1,56, 1,94 bzw. 2,71. Die erste Linie gab in X_2 1,00 und in X_3 0,80, die zweite 1,78 bzw. 1,18 und die dritte 2,79 bzw. 2,40. Die Keimungsunterschiede zwischen spaltenden und nicht spaltenden Parzellen waren äusserst klein.

Die χ^2-Analyse der Spaltungen ergibt folgendes Resultat:

		D.F.
$\Sigma\ \chi^2$ der summierten Spaltungszahlen	$= 23{,}81^{***}$	1
Het. *zwischen* Parz. in X_3 oder zw. Pfl. *innerhalb* d. Parz. X_2	$= 53{,}71$ —	51
» » » » X_2 » » » » » X_1	$= 52{,}57^{*}$	34
» » » » X_1 » » » » » X	$= 31{,}29^{***}$	10
» » » » X	$= 15{,}88^{*+}$	6
» » Generationen	$= 2{,}56$ —	2
$\Sigma\Sigma\ \chi^2$	$= 179{,}82^{***}$	104

Das Resultat der χ^2-Analyse könnte folgendermassen erklärt werden: Vielleicht besteht ein Unterschied zwischen den verschiedenen Mutationen in diesem morphologischen Typus in bezug auf den Ursprung, wodurch sich dann in der ersten Generation eine gewisse Selektion geltend macht (wahrscheinlich eine Gametenelimination; vgl. unten!). Die Variationsanalyse von *Samen je Hülse* in X_2-Parzellen geht in dieselbe Richtung wie dies bei *chr—a* und *chr—l* der Fall war. Der Quotient *zwischen/innerhalb* der Parzellen ist $8{,}30^{***}$ mit einem M-Quadrat von 8,96, D.F. = 22 und 1,08, D.F. = 308, was eine Ausdifferenzierung von verschiedenen Fertilitätslinien anzudeuten scheint.

Die Mutante chr—g (*Chlorina-Typus*?). — Diese Mutante ist nur einmal aufgetreten. Sie gleicht im grossen RASMUSSONS (1938) *ch—g*, aber man kann sie auch mit GUSTAFSSONS (1938, 1940) »*Tigrina*»-Typus der Gerste vergleichen. *chr—g* ist anfangs hellgrün (»*Chlorina*-grün»). Typisch ist, dass die Blättchen sich nicht ganz entwickeln (Fig. 3 *e*). Bei 4 bis 5 Blattpaaren und 1—1,5 dm Höhe bekommt die Chlorophyllpflanze einen wässrigen grau-hellgrünen Farbenton. Die Ränder der Blättchen beginnen zu welken (sie verlieren das Chlorophyll und werden heller, zeigen aber keine Gelbfärbung) und rollen sich mehr und mehr gegen die Mitte ein. Nach und nach wird die Pflanze noch heller und verwelkt mehr oder weniger eingerollt, ohne gelb zu werden. Sie lebt 2 bis 3 Wochen und ihr Lebensablauf ist sehr charakteristisch. Die Gesamtspaltung war $0{,}818 \pm 0{,}083$ Rez. je 4 mit 436 Individuen. Diff./m = 2,2. Die verschiedenen Generationen zeigten ein ähnliches Bild. Die Anzahl nicht spaltender Parzellen ist hier auch normaler als bei irgendeinem der anderen Typen, die in dieser Abhandlung beschrieben sind: im Durchschnitt 1,12 für X_2 und X_3. Die Keimung zeigte keinen Unterschied zwischen den Parzellen der Typen. Die χ^2-Analyse der Spaltung deutete einen schwachen Mangel an Rezessiven an: $4{,}88^{*}$, D.F. = 1, indem eine gewisse Heterogenität nur *zwischen* den Pflanzen *innerhalb* X_2 zu verspüren ist ($15{,}57^{**}$, D.F. = 6). Diese Heterogenität hängt wahrscheinlich mit der Empfindlichkeit des Typus gegen Witterungsverhältnisse zusammen, denn die Variationsanalyse von *Samen je Hülse* in X_2-Parzellen gab nicht die geringste Andeutung für Unregelmässigkeiten in der Fertilität zwischen den Parzellen.

DIE ALLGEMEINE GENETIK DER RÖNTGENMUTATIONEN.

Zu einer Analyse von speziellen Erscheinungen in der Chlorophyllgenetik eignet sich nur die *Uni*-Serie wegen ihren grösseren Umfanges, weshalb hier nur diese Serie besprochen werden soll.

Dass ein prinzipieller Rezessivenmangel vorhanden ist, erscheint offenbar, wenn man die verschiedenen Spaltungszahlen betrachtet. Natürlich zeigt die gesamte Mutantenspaltung dasselbe: 5444 grüne : 1261 cx., was für je 4 $0{,}752 \pm 0{,}021$ mit Diff./m = 11,8 gibt. Wenn wir die verschiedenen Typen betrachten, so finden wir, dass alle ausser *chr—g* einen Rezessivenmangel geben, der $P < 0{,}001$ entspricht; *chr—g* gibt $P = 0{,}05$. Die gesamte Heterogenität der Spaltungen, berechnet nach der χ^2-Methode, ergibt bei Vereinigung sämtlicher Typen folgendes Bild:

		D.F.
$\Sigma\,\chi^2$ der summierten Spaltungszahlen	$= 137{,}55^{****}$	1
Het. *zwischen* Parz. in X_3 oder zw. Pfl. *innerhalb* d. Parz. X_2	$= 112{,}84$ —	103
» » » » X_2 » » » » » X_1	$= 114{,}84^{****}$	68
» » » » X_1 » » » » » X	$= 37{,}07^{**}$	19
» » » » X	$= 42{,}00^{***}$	16
» » Generationen	$= 19{,}43^{*}$	10
» » Spaltungszahlen der Chlorophylltypen	$= 43{,}30^{***}$	4
$\Sigma\Sigma\,\chi^2$	$= 507{,}03^{****}$	221

Aus dieser Übersicht geht hervor, teils dass die gesamte Spaltungssumme eine entschieden gestörte Normalverteilung zeigt sowie dass verschiedene Mutanten nicht dasselbe Spaltungsbild aufweisen, teils auch dass innerhalb desselben Mutantentypus in den spaltenden Generationen eine erhebliche Heterogenität vorhanden ist. Die Ursache der unnormal grossen Heterogenität in X_2 dürfte zu grösstem Teil in den schlechten Keimungsbedingungen von 1939 zu suchen sein.

Eine Untersuchung des Verhaltens der spaltenden zu den nicht spaltenden Parzellen ergibt nach der χ^2-Analyse folgendes:

		D.F.
$\Sigma\,\chi^2$ der summierten Spaltungszahlen	$= 2106{,}23^{****}$	1
Het. *zwischen* Generationen innerhalb der X-Parzellen	$= 242{,}92^{***}$	22
» » X-Parzellen	$= 81{,}95^{***}$	6
» » Chlorophylltypen	$= 5{,}90$ —	4
$\Sigma\Sigma\,\chi^2$	$= 2437{,}00^{****}$	33

Die Differenz der Mittelwerte von χ^2 für spaltende und nicht spaltende Parzellen *zwischen* X_1 und jenen des Durchschnittswertes von $X_2 + X_3$-Generationen beträgt $178{,}3 \pm 25{,}1$, was ein Diff./m von 7,10 gibt; *zwischen* X_2 und X_3 ist die Differenz $21{,}72 \pm 5{,}02$ mit Diff./m = 4,33. Eine Variationsanalyse der Zahlen je 3 gibt ein ähnliches Resultat, das aber nicht so markant ist. Wenn die Jahrgänge als Fehler aufgefasst werden, so wird der Quotient für *zwischen* X-Parzellen = 2,18 mit

$0{,}05 < P < 0{,}01$, für *zwischen* Chlorophylltypen: $2{,}58$ mit $P = 0{,}05$ und zwischen *zwischen* und *innerhalb* X-Parzellen: $1{,}66$ mit $P = 0{,}05$. Bei einer Untersuchung des Verhaltens der χ^2-te *innerhalb* der drei Generationen geht deutlich hervor, dass diese sich von abnorm hohen Werten allmählich erniedrigen, was die Nummer der Generation anzeigt, aber auch dass die Variation innerhalb der Jahrgänge gleichzeitig zunimmt (Mittelwert χ^2: $X_1 = 194{,}00$, $\sigma = 65{,}1$; X_2: $26{,}57$, $\sigma = 18{,}9$ und für X_3: $4{,}85$ mit σ $5{,}1$).

Wenn man diesen Ausleseprozess zwischen spaltenden : nicht spaltenden Parzellen mit der Tabelle für die χ^2 der gesamten Spaltungszahlen auf der vorherigen Seite und die Chiquadratberechnung für jede einzelne Mutante vergleicht, so zeigen die statistischen Berechnungen in folgende Richtung: *Durch die Röntgenbehandlung sind in der X-Generation gleichzeitig mehrere individuelle Mutanten von gleichem morphologischen Aussehen entstanden und während den folgenden Generationen hat ein selektiver Prozess stattgefunden.* Endgültige Antwort auf diese Fragen können indessen nur eine genetische Kreuzungsanalyse und ein schwer durchzuführender Ausleseversuch geben.

Der oben erwähnte Ausleseprozess könnte entweder auf die Gameten oder auf die Zygoten einen Einfluss haben.

Dass indessen Zygotenletalität als Erklärung dieser Auslese weniger wahrscheinlich ist, zeigte u. a. eine Variationsanalyse des Keimungsprozentes. Diese Analyse umfasste den Einfluss verschiedener X-Parzellen (=Röntgeneffekt), verschiedener Generationen, von Homo- oder Heterozygoten, sowie die gegenseitige Beeinflussung dieser auf die Keimung; auch eine Berechnung des Einflusses von Unterschieden im Chlorophylltypus wurde vorgenommen. Nur zwischen verschiedenen Generationen, d. h. Jahrgängen, war ein entschiedener Einfluss auf die Keimung zu finden ($0{,}01 < P < 0{,}001$). Es war X_2 (1939) mit seinen schlechten Keimungsbedingungen, das die Abweichung zeigte. Aber es war schon früher bekannt, dass Chlorophyllpflanzen von *Pisum* im allgemeinen schneller keimen als grüne, was auch durch wiederholte Aufgehenbeurteilungen in diesem Material bestätigt wurde, weshalb der schlechteren Keimung in X_2 kein entscheidender Einfluss auf die Erörterung der Ursachen der Letalität zuzuerkennen sein dürfte. Der Gesamtdurchschnittswert der Keimung einer spaltenden Parzelle beträgt $73{,}0$ % und einer nicht spaltenden $65{,}4$ %; der entsprechende Wert für $X_2 = 58{,}7$ % und der für $X_3 = 79{,}9$ %. Nach der Analyse sind also in der Keimung keine Unterschiede nachzuweisen; die Wahrscheinlichkeit einer Zygotensterilität als Ursache der Familienauslese erscheint daher

noch geringer. Gametenstörungen sind also am naheliegendsten. HALLQVIST (1924) gibt Beispiele für ähnliche Störungen in einer spontanen *Albina*-Mutation der Gerste an, die er als eine Gametenmutation erklärt, die später in den Nachkommenschaften ausgelesen wird. Wie später gezeigt wird, ist unser Fall, wenn diese Auffassung richtig ist, ein ausgeprägter solcher.

Für die X_2-Generation der *Uni*-Serie ist eine statistische Analyse über den Einfluss der Fertilität auf verschiedene Faktoren ausgeführt worden. Als Basis wurde die Anzahl *Samen je Hülse* benutzt. Hierbei zeigte sich, dass die Variation 1) *zwischen* den Mutantentypen $2{,}30$ mit D.F. $= 4$ ist, 2) *zwischen* Parzellen *innerhalb* der Mutantentypen $6{,}47$ mit D.F. $= 46$ und 3) *zwischen* Pflanzen *innerhalb* von Parzellen (Fehler) $1{,}02$ mit D.F. $= 701$. Der Quotient für $1 : 3$ ist $2{,}25^*$ und für $2 : 3 = 6{,}34^{***}$. Mit Hinsicht auf die Durchschnittszahlen Samen je Hülse können die Mutantentypen in zwei Gruppen eingeteilt werden, die sich indessen nicht sicher voneinander unterscheiden. Die erste Gruppe umfasst *chr—a* mit $3{,}16 \pm 0{,}26$ Samen je Hülse und *chr—o* mit $3{,}28 \pm 0{,}19$, und die zweite Gruppe die übrigen, nämlich, *chr—d* mit $3{,}62 \pm 0{,}17$, *chr—l* mit $3{,}59 \pm 0{,}21$ und *chr—g* mit $3{,}61 \pm 0{,}063$. (Man beachte den kleinen mittleren Fehler, obgleich n nur 69 beträgt). Zum Vergleich sei erwähnt, dass die unbehandelte Normallinie $4{,}53 \pm 0{,}073$ Samen je Hülse gibt. Untersucht man, ob die Variation innerhalb der verschiedenen Mutantentypen ungleich ist, so erhält P für den Quotienten zwischen *zwischen* Parzellen und *innerhalb* Parzellen folgende Werte: *chr—g* $> 0{,}02$, *chr—a* und *chr—l* $< 0{,}01$ und *chr—d* und *chr—o* $< 0{,}001$. Dieses Bild einer Analyse *innerhalb* der morphologisch gleichen Mutanten gleicht deutlich dem der χ^2-Analyse der Spaltungen *innerhalb* jeder Mutation.

Auch die Fertilitätsunterschiede *zwischen* homozygoten und heterozygoten Pflanzen in X_2 wurden studiert. Dies geschah mit Hilfe der Spaltungszahlen von X_3 für die Familien aus X_2; die Anzahl *Samen je Hülse* von homozygoten und heterozygoten Pflanzen in X_2 wurden je für sich beurteilt. Diff./m aus der Gesamtsumme in dieser Weise berechnet gibt $0{,}91$ mit $P = 0{,}4$. Für den Unterschied *zwischen* den spaltenden und nicht spaltenden Parzellen *innerhalb* der verschiedenen Mutantentypen wurde eine ebenso kleine Sicherheit beobachtet. Der Durchschnittswert *Samen je Hülse* der heterozygoten Pflanzen in X_2 scheint mit χ^2 für die Spaltung in X_3 keinen Zusammenhang zu haben.

BEHANDLUNG KONTRA MUTATIONSTYPEN.

Auch in diesem Fall ist nur die *Uni*-Serie gross genug, um eine Prüfung in dieser Hinsicht zu gestatten. In bezug auf das Auftreten der verschiedenen Mutationstypen bei variierenden Röntgendosen ist folgendes zu erwähnen. Zu berücksichtigen ist hierbei, dass das geringe Versuchsmaterial keine allgemeinen Schlüsse über eine eventuell ausgeprägte Reaktion von *Pisum* auf X-Strahlen zulässt. Eine Besonderheit kann jedoch mit ziemlicher Sicherheit hervorgehoben werden, dass nämlich keine wirklichen *Albina*-Typen beobachtet worden sind. In der *Acacia*-Serie trat allerdings ein genetisch bedingter *Albo*-Chimärentypus, *chr—w*, auf, der aber in seinem ersten Stadium nicht ganz weiss war. Sämtliche *Xantha*-Typen und 75 % der *Lutescens*-Typen sind bei der niedrigsten Bestrahlungszeit (5 Stunden) aufgetreten. Bei der längsten Zeit (9 Stunden) sind nur *Viridis*-Typen beobachtet worden. Der Metabolismus wirkt ungefähr in derselben Weise ein, wie es GUSTAFSSON (1940) für die Gerste beschrieben hat. So treten gleich viele *Virescens*- und *Viridis*-Typen in den beiden Metabolismustypen auf, während 80 % der *Xantha*-Typen in der gequollenen Gruppe erscheinen. *chr—g*, die ich mit dem »*Tigrina*»-Typus von GUSTAFSSON verglichen habe, trat in trockenen Samen auf. Ein Unterschied bestand jedoch darin, dass alle *Lutescens*-Mutanten mit trockenen Samen erhalten worden sind.

DIE FREQUENZ DER VERSCHIEDENEN CHLOROPHYLLTYPEN.

Welche Chlorophylltypen bei *Pisum* durch X-Strahlen zutagekommen, geht aus dem oben Erwähnten hervor. Finden wir aber dieselben Typen innerhalb der spontanen Variation der Mutanten, wie dies z. B. bei *Hordeum* der Fall ist? Leider sind diesbezüglich nur wenige Beobachtungen veröffentlicht. Ich bin jedoch der Ansicht, dass die Chlorophyllmutationen bei *Pisum* nicht seltener sind als bei *Hordeum* oder *Zea*.

In der Literatur habe ich folgende spontane Mutationen erwähnt gefunden: DE HAAN (1930) 1 unsichere *Albo*-Chimäre und 2 maternell vererbte *Xantho*-Chimären und derselbe (1933) 1 *Xantha*; BATESON und PELLEW (1916) 1? *Albina*?; WHITE (1917) 1 *Viridis*; NEFF und WHITE (1927) 1? *Viridis*; FRUWIRTH (1920) 1 *Albina*, 1 genetische *Albo*-Chimäre und 1 maternelle *Xantho*-Chimäre; SPRENGER (1916) nach DE HAAN (1933) 1? maternelle? *Albo*-Chimäre? (dieser Fall erscheint besonders unsicher); KAJANUS (1919) 1 maternelle *Xantha*-Chimäre; und schliess-

lich RASMUSSON (1929) 1 *Albina* und 2 *Lutescens* und derselbe (1938) 3 *Xantha*, 1 *Lutescens* und 4 *Viridis*-Typen.

Ausserdem können hier einige neue Beobachtungen mitgeteilt werden. RASMUSSON (nicht veröff.) hat mir gütigst mitgeteilt, dass er ausser den vorher publizierten Mutanten noch einige andere besitzt, nämlich 2 *Xantha*, 4 *Lutescens* und 3 *Viridis*, die alle als individuelle Mutationen aufgetreten sind. Ferner habe ich während der zwei Sommer 1936 und 1937 mit gütigster Genehmigung des damaligen Vor-

TABELLE 2. *Die Frequenz der Chlorophylltypen.*

Ursprung	*Albina*	*Xantha*	*Lutescens*	*Chlorina*	*Chimären*		Summe
					Albina-viridis	*Xantha-viridis*	
Pisum, spontane	3?	38	36	51	2	9?	139
%	2	27	26	37	1	7	100
d:o Röntgen	0	3	6	11	1	0	21
%	0	15	27	54	4	0	100
d:o Summe	3	41	42	62	3	9	160
%	2	25	25	40	2	6	100
Hordeum, spontane ...	7	4	5	2	—	—	18
%	39	22	28	11	—	—	100
d:o Röntgen	162	34	0	100	61	7	364
%	45	9	0	27	17	2	100
d:o Summe	169	38	5	102	61	7	382
%	44	10	1	27	16	2	100
Verschiedene Pflanzengattungen	24	22	20	30	18		114
%	21	19	18	26	16		100
(DE HAAN, 1933)							

stands der Staatlichen Gemüseversuche in Alnarp, Agronom Å. NYHLÉN, Gelegenheit gehabt sämtliche zur Kontrolle gebauten, verschiedenen Handelslinien durchzugehen, um eine weitere Auffassung von dem spontanen Auftreten von Chlorophylltypen bei *Pisum* zu bekommen. Beide Jahre wurden mehr als 200 Tausend Pflanzen, die eine sehr grosse Anzahl von Linien umfassten, durchgegangen. Alle Mutationen, die auf diese Weise vermerkt wurden und deren Entwicklung während des ganzen Lebens jedes Individuums verfolgt wurde, um es so sorgfältig wie möglich zu klassifizieren, können nicht als individuelle Mutationen aufgefasst werden. Wenn wir aber die Weise, in der diese Kontrollproben einer sehr grossen Population entnommen wurden, berück-

sichtigen, so wird es wahrscheinlich, dass sie doch ein ziemlich gutes Bild von der gegenseitigen Frequenz geben. Der Lebenswert der verschiedenen Typen hat sicher einen Einfluss durch Selektion, indem vor allem die grünen Typen ein wenig überrepräsentiert werden. Im Jahre 1936 wurden 19 *Xantha*, 19 *Lutescens*, 19 *Viridis* und 1 *Xantha*-Chimäre, oder insgesamt 58 Chlorophyllpflanzen beobachtet. Im Jahre 1937 vermerkte ich 13 *Xantha*, 10 *Lutescens*, 23 *Viridis* und 4 *Xantha*-Chimären (eine von diesen ist kaum von dem *Albo*-Chimärentypus zu unterscheiden), insgesamt 50. Tabelle 2 gibt eine Übersicht über die Mutationstypen von spontanen und X-induzierten Mutationen von *Pisum* nach oben Erwähntem und zum Vergleich mit *Hordeum* nach GUSTAFSSON (1938, 1940). Ausserdem sind auch die Frequenzen dieser Typen für verschiedene Pflanzengattungen nach Tabellen von DE HAAN (1933) aufgenommen worden. Für jeden Ursprung sind auch die Prozentzahlen berechnet.

Aus dieser Tabelle ergeben sich einige interessante Daten. So zeigt die Gattung *Pisum*, worauf schon früher hingewiesen wurde, im grossen keine *Albina*-Formen. Dies kann indessen andere Konsequenzen haben, worauf später zurückgekommen werden soll. Desgleichen gibt es äusserst wenige *Albo*-Chimären, aber mehrere *Xantha*-Chimären. Die *Chlorina*-Typen sind bei der Erbse ungewöhnlich reich vorkommend, sowohl innerhalb der spontanen als der röntgeninduzierten Gruppe, weshalb eine eventuelle Überschätzung im Alnarpmaterial nicht so gross sein kann. Ausserdem sind die *Lutescens*-Typen von *Pisum* ebenso wie in den übrigen Pflanzengattungen, ausser *Hordeum*, relativ häufig [ein X-induzierter *Lutescens*-Typus wird jedoch von GUSTAFSSON (1941) angeführt].

Aus den obigen Mitteilungen könnte vielleicht irrtümlich gefolgert werden, dass bei *Pisum* nur Chlorophyllmutationen und keine anderen morphologischen Formen auftreten können. Die Literatur gibt indessen mehrere Fälle an. LAMPRECHT (1939) berichtet über 11 Mutationen, alle mit grösserem oder geringerem Effekt auf die Blüte und die Fertilität und ausserdem mit Blattdeformationen; RASMUSSON (1938) veröffentlicht eine ähnliche Mutation mit trichterförmigen Blättern. Eine identische Form ist laut RASMUSSON von DELWICHE und RENARD (1926) veröffentlicht worden. Ausserdem berichtet RASMUSSON über zwei »*Status*»-Mutationen. In meinen Kreuzungsnachkommen sind (unveröff.) zwei ähnliche »*Status*»-Typen aufgetreten, die entweder spontane Mutationen (in diesem Fall Komplexmutationen) oder das Ergebnis von Kreuzungskomplikationen sind. Im Alnarpmaterial habe ich

auch eine ganz wachslose Pflanze gefunden, die mit grosser Sicherheit als spontane Mutation aufgefasst werden muss. Weiter sind in dieser Hinsicht alle rezessiven Eigenschaften von ursprünglichen praktischen und theoretischen Linien zu erwähnen.

Es ergibt sich demnach, dass bei *Pisum* auch andere Mutationen als Chlorophylltypen auftreten, obgleich sie eine niedrigere Frequenz zu zeigen scheinen. In meinen Röntgenexperimenten sind indessen nur Chlorophyllmutationen aufgetreten.

BESPRECHUNG DER ERGEBNISSE.

Die Reaktion der Gattung *Pisum* auf X-Strahlen scheint also nach dieser Untersuchung im grossen nach den Prinzipien stattzufinden, die TIMOFÉEFF-RESSOVSKY (1937) dargelegt hat oder die laut den grossen Arbeiten GUSTAFSSONs zu erwarten wären. Bei *Pisum* scheint jedoch nur geringe Sterilität aufzutreten. Weitere Röntgenversuche würden aber vielleicht ein ähnliches Verhalten wie bei *Hordeum* zeigen, d. h. dass alle Grade von Sterilität gefunden würden, wofür eine Untersuchung von KRAJEVOJ (1935) spricht.

Interessant ist die *genetisch bedingte Variegata-Form*, die in der *Acacia*-Serie aufgetreten ist. Über eine spontane Mutation von identisch demselben Typus berichtet, wie schon erwähnt, FRUWIRTH (1920). Seine gesamten Spaltungszahlen zeigen, dass auch in diesem Fall ein Rezessivenmangel vorhanden ist ($0{,}56 \pm 0{,}047$ Rez. je 4; Diff./m $= 9{,}2$). Eine eigenartige Erscheinung bilden die von ihm beschriebenen »übersprungenen», spaltenden Generationen, d. h. eine spaltende Parzelle hat in einigen Fällen keine spaltenden Nachkommen gegeben, die indessen in *ihren* Nachkommenschaften gespalten haben, nun aber mit einem sehr grossen Rezessivenmangel. Die »übersprungenen» Generationen könnten vielleicht durch einen Wegfall von Chlorophyllpflanzen oder durch zu geringe Individuenanzahl je Familie erklärt werden, d. h. als versteckt spaltende Parzellen. Bei einem Vergleich von Fällen in der Literatur mit eigenen Beobachtungen finde ich, dass die genetisch bedingten *Variegata*-Typen am stärksten diminutiv und in rezessivem Zustand schwer reproduzierbar sind, während die maternell vererbten sich in bezug auf Vitalität von den normalen Pflanzen nur wenig unterscheiden.

Eine augenfällige Erscheinung bei einem Vergleich von *Pisum*-Mutationen mit solchen anderer Gattungen ist *der beinahe vollständige Mangel an Albina-Typen*. Einige spontane Fälle sind indessen bekannt,

aber nicht alle von diesen können als sicher aufgefasst werden. Denn nach Beobachtung des Verfassers zeigt es sich, dass Chlorophyllpflanzen bei Erbsen, die man auf den ersten Blick als weiss klassifizieren möchte, nicht ganz weiss sind, sondern mehr oder weniger Karotin enthalten. Dies könnte auch bei einigen der älteren *Albina*-Angaben der Fall sein. Der *Variegata*-Typus des Verf:s zeigte anfangs eine gelbweisse Farbe, die später in eine ganz weisse überging. In anderen Pflanzengattungen treten aber ganz weisse *Albina*-Typen auf. In erwähnter Hinsicht scheint der Mais der Erbse am nächsten zu stehen, obwohl auch hier viele reine *Albina*-Typen vorkommen. In F_2 von Kreuzungen zwischen verschiedenen *Pisum sativum*-Linien und *Pisum abyssinicum* (VON ROSEN, 1942 und unveröff.) erschienen mehrere Chlorophyllpflanzen. Ihr morphologisches Bild variiert jedoch wenig; etwa 75 % gleichen *chr—y*, und die übrigen sind teils mit *chr—d*, teils mit *chr—o* vergleichbar. Auch hier traten keine *Albina*-Typen auf.

Bemerkenswert für beinahe alle hier aufgetretenen Mutationsformen ist *der grosse Rezessivenmangel*. Nur die Gesamtspaltungszahlen von *chr—w* und *chr—g* geben bei der χ^2-Analyse einen P-Wert, der grösser als 0,001 ist. Auch die Röntgenmutation *chr* von RASMUSSON (1938) zeigt ein ähnliches Bild. In anderen Pflanzengattungen aber scheint der Rezessivenmangel nicht von solcher Grösse zu sein, oder auch geben verschiedene Mutationstypen nicht denselben Rezessivenmangel. So gibt GOODSPEED (1930) die Ausspaltung einer röntgeninduzierten *Albina*-Mutation in *Nicotiana* zu $0{,}98 \pm 0{,}065$ je 4 an. Bei *Hordeum* zeigen die grünen Mutationen den grössten Mangel, während bei *Phleum* (WEXELSEN, 1941) das Umgekehrte der Fall ist. Bei *Pisum* zeigen dagegen die *Xantha*-Typen den grössten Mangel. Bei einer Übersicht der Literatur ergibt sich, dass im ganzen *Xantha* und *Viridis* das grösste Rezessivendefizit aufweisen. Da *Albina*-Typen bei *Pisum* kaum auftreten, kann hier über ihr Verhalten kein Vergleich angestellt werden.

Die letzte Frage führt eine andere Seite der Probleme in den Vordergrund, nämlich die, warum *Albina*-Typen bei *Pisum* so selten sind. Von GUSTAFSSON (1940) sind die *Albina*-Formen als *intragenische* (= eigentliche Genmutationen), die *Xantha*- und *Viridis*-Formen dagegen als *intergenische* Mutationen (= Makro- oder chromosomale Aberrationsmutationen) erklärt worden. KRAJEVOJ und RASSULI (1935; auch LUTKOV, 1937) beschrieben *Translokationen* und *Fragmentationen* nach Röntgenbestrahlung von Erbsen, weshalb man bei *Pisum* vielleicht mit Recht auch von ähnlichen Verhältnissen sprechen darf. Aber dann

müsste angenommen werden, dass die *Gene von Pisum gegen X-Strahlen sehr unempfindlich wären, da nur Chromosomenaberrationen auftreten.* ATABEKOWA teilt 1936 und 1937 auch einige Beispiele für *Kern-* und *Polyploidie-Störungen* mit, was in dieselbe Richtung zeigt.

Wenn das Verhalten berücksichtigt wird, dass gewisse Chlorophyllmutationen in X_1 nur in einzelnen spaltenden Parzellen und als einzelne cx-Pflanzen auftreten, während andere sich ziemlich normal verhalten, könnte ein Vergleich mit ähnlichen Erscheinungen bei der Gerste laut HALLQVIST (1924) und bei einem prinzipiellen Vergleich mit TIMOFÉEFF-RESSOVSKYS Ergebnissen (1937, S. 33) vielleicht einen bestimmten Bescheid geben. Nach dem letztgenannten gibt eine Mutation ungleiche genetische Bilder in den ersten spaltenden Generationen, abhängig von dem Zustand des Samens oder des Stadiums des Keimlings, in dem die Bestrahlung eingewirkt hat. Eine Mutation, die im *primären* Embryostadium eingetroffen ist, gibt eine *Gesamtmutation*, während eine im *sekundären* Embryostadium eingetroffene ein *Chimärenbild mit selektivem Wert* bedingt. Wichtige Auskünfte über die unmittelbare Wirkung des Mutationseffektes geben auch die Keimungsresultate und die Fertilität während mehrerer Generationen. Wird das vorliegende Material von diesem Gesichtspunkt aus beleuchtet, so ist man geneigt, diese *Mutationen dem Ursprung nach in zwei Gruppen* einzuteilen:

Die Chlorophylltypen *chr—d*, *chr—a*, *chr—l* und die Linie 804/1936 von *chr—o* sollten als *sekundäre Mutationen im Gametenstadium* entstanden sein. Dies sind nämlich Formen, die nach mehreren Berechnungsweisen in den Nachkommen den grössten Auslesewert zeigen, verursacht durch eine Elimination von letalen Gameten. Die zweite Gruppe umfasst die Linien 807/ und 808/1936 von *chr—o* sowie ferner *chr—g*, *chr—w* und *chr—y*, die dann als *Komplexmutation im Primärstadium* aufzufassen wären und wahrscheinlich auch im Gametenstadium entstanden sind. *Nur für chr—w ist es schwer zu entscheiden, ob sie eine intra- oder intergenetische Mutation darstellt.* Eine weitere Bestätigung der obigen Annahmen scheinen die Veröffentlichungen mehrerer Forscher, z. B. STUBBE, KAPLAN, LUTKOV u. a. zu bilden, dass der Pollen gegen X-Strahlen besonders empfindlich ist.

Die Resultate dieser Untersuchung sprechen auch für eine *Gametenelimination als Ursache der grossen Abweichungen der Spaltungen*, ein Schluss zu dem auch GUSTAFSSON in bezug auf *Hordeum* gekommen ist.

Es ist mir ein Vergnügen, denen, die diese Untersuchung ermöglicht haben, meinen herzlichsten Dank auszusprechen. Ich danke dem Genetischen Institut der Universität zu Lund und der Schwedischen Zuckerfabriks-A.G. und besonders Prof. H. NILSSON-EHLE, Svalöf und Dr. J. RASMUSSON, Hilleshög.

Hilleshög im Oktober 1941.

SUMMARY.

1. An investigation of the effect of X-rays on *Pisum sativum* was carried out. The material was studied both from a physiological and a genetical point of view.

2. The physiological effect caused by the X-rays is what was to be expected from our knowledge of the effect in other plant families.

3. Only chlorophyll mutations appeared, which the *xantha*, *lutescens* and *chlorina* groups represented, and a genetical *albo-viridis* chimaera was also found. It is of special interest that in the 22 chlorophyll mutations obtained no *albina* type appeared. All mutations segregate in the ratio of 3 : 1.

4. The occurrence of spontaneous *Pisum* mutations is discussed. Here *albina* types are found, but only a few cases.

5. The segregation numbers show a great lack of recessive plants in 5 out of 7 chlorophyll types. The same thing is true of the numbers of segregating plots. A weak sterility is present, but no differences in germination were ascertained.

6. A statistical analysis of the material has been made.

7. Several factors in the results point to the conclusion that gametic and not zygotic elimination is the cause of some disturbances.

8. Only macromutations are assumed to have caused the occurring mutations.

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EIN EIGENTÜMLICHER FALL VON GYNANDROMORPHISMUS

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DIE Literatur enthält eine Menge Beschreibungen von Gynandromorphen verschiedener Tierklassen. Ein besonders reichliches Material zu diesen Deskriptionen haben die Schmetterlinge geliefert. In der Regel entbehren sie allgemein biologisches Interesse. Erst durch die Entdeckung der Geschlechtschromosomen und des Mechanismus der Geschlechtsbestimmung gewannen die Gynandromorphen Bedeutung für die allgemeine Biologie. BOVERI, MORGAN und DONCASTER haben Erklärungen zur Entstehung der Gynandromorphen in verschiedenen Insektenordnungen gegeben. GOLDSCHMIDT (1923, 1927 b), der sich hauptsächlich für das Problem der Intersexualität interessiert hat, hat auch Zeit gefunden erblich bedingte Fälle von Gynandromorphismus eingehender zu studieren und hat in erster Linie dazu beigetragen die Begriffe des Gynandromorphismus und der Intersexualität aufzuklären. In keiner Arbeit der genannten Verfasser habe ich indessen einen ähnlichen Fall wie denjenigen von mir entdeckten finden können. Während die erwähnten Fälle sich in erster Linie auf das Soma beziehen oder sogenannte Ovotestes behandeln, handelt es sich in meinem Fall um einen Gynandromorphismus in einem ganz kleinen Teil der Keimbahn.

Bei meinen Bemühungen mir Material von den beiden Lepidopteren *Pygaera pigra* HUFN. und *P. curtula* L. anzuschaffen um meine Untersuchungen über die Keimzellenbildung der Bastarde zwischen diesen Arten von neuen Gesichtspunkten aus zu revidieren, entdeckte ich bald, dass zahlreiche Populationen dieser Arten durch Inzucht nicht fortgepflanzt werden können. Ich vermutete das Vorkommen von verschiedenen Letalfaktoren, denn in einigen Zuchten gingen schon die Eier zu Grunde, in anderen erst die erwachsenen Raupen. Diese hörten auf zu fressen, vermochten sich jedoch nicht zu verpuppen und starben schliesslich ohne eigentliche Krankheitssymptome zu zeigen (FEDERLEY, 1941). Im Sommer 1941 gelang es mir endlich, trotz schwieriger äusserer Verhältnisse, die reziproken Bastarde zwischen *pigra* und *curtula* zu erzielen. Um Material zu erneutem Studium der Spermatogenese der Bastarde zu erhalten, fixierte ich Testes der Raupen in verschiedenen

Fixierungsmitteln (CARNOY, BENDA, BOUIN) und als Vergleichsmaterial Testes der reinen Arten, die aus demselben Material stammten. Dieses war von mir im Sommer 1940 im Kirchspiel Snappertuna auf den Inseln Dalkarö-Lillö und Dalkarö-Storö gesammelt worden und ist in bezug auf das Vorkommen von Letalfaktoren und Parasiten von mir eingehend beschrieben worden (FEDERLEY, 1941).

Leider wurden nur drei Paare *pigra*-Testes fixiert, alle in dem Gemisch von BENDA. Alle sechs Testes zeigten verschiedene mehr oder weniger abnorme Chromosomenverhältnisse, die sicher für die Sterblichkeit der Eier und vermutlich auch der Raupen verantwortlich gemacht werden können. Diese an und für sich hochinteressanten Eigentümlichkeiten werde ich in anderem Zusammenhang behandeln und werde mich auch bemühen, wenn die politischen Verhältnisse es gestatten, mir neues und reichhaltigeres Material von derselben *pigra*-Population zu verschaffen. Hier soll nur eine Abnormität, der Gynandromorphismus in den Testes der einen Raupe, beschrieben und diskutiert werden.

Die Testes wurden kurz vor der letzten Raupenhäutung fixiert. Morphologisch sind sie vollständig normal, sie zeigen die charakteristische Nierenform und bestehen aus vier gut entwickelten Follikeln. Diese sind schon zum grössten Teil von reifen und halbreifen Spermien erfüllt, aber in der Nähe der Apicalzellen kommen noch Spermatogonien und junge Spermatozyten vor. Auch pachytäne Stadien sowie Diakinesen und Reifeteilungen konnten noch gefunden werden, obgleich sie nicht mehr häufig sind. Im grossen und ganzen machen die beiden Testes einen durchaus normalen Eindruck, wenn wir von den anomalen Chromosomenverhältnissen absehen.

In einem Follikel fielen indessen einige Zellen durch ihre Riesengrösse auf. Ein näheres Studium derselben ergab, dass es sich um eine regelrechte Oozyte mit ihren sieben Nährzellen handelt, die alle von einem typischen Zystenepithel umgeben sind und so eine freie Zyste bilden. Die Oozyte befindet sich noch in einem jungen Stadium. Die Chromosomen sind schlank und lang, nur schwach chromatisch und vom Lampenputzer-Typus. Die Nährzellen haben sehr grosse Kerne mit sehr zahlreichen Chromatinkörnern und wenigen kleinen Nukleolen. Die Form der Kerne ist in der Hauptsache rund, nur an der einen Seite kommen die Lappen und Einbuchtungen zum Vorschein, die in einem späteren Entwicklungsstadium so charakteristisch sind. Die Form der Zelle selbst ist auch rundlich und die Zellen liegen nicht so dicht aneinander gedrückt, wie in einem späteren Stadium der Oogenese. Die

Zyste befindet sich allem Anschein nach in einem ziemlich jugendlichen Stadium der Entwicklung. Vergl. untenstehende Abbildungen.

Eine Durchmusterung des anderen Testis ergab das überraschende Resultat, dass auch dieser eine ganz identische Zyste mit einer jugendlichen Oozyte und sieben Nährzellen enthält. Auch hier liegt die Zyste frei im Follikel ohne jede Verbindung mit den übrigen Zysten oder der Follikelwand.

Wie soll nun das Vorkommen einer solchen Zyste mit einer jungen Oozyte und sieben Nährzellen in einem sonst normal gebauten Testis, und zwar sowohl in dem linken als in dem rechten, erklärt werden?

Zunächst möchte ich hervorheben, dass die Zysten in der Haupt-

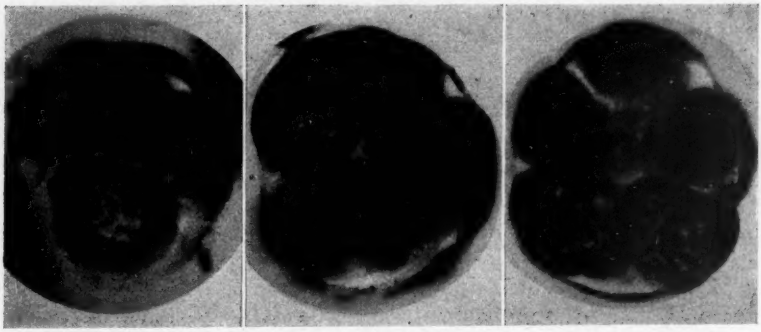

Fig. 1. Drei Schnitte durch die Oozyste; links: die Oozyte mit den langen Chromosomen (unten) und zwei Nährzellen; in der Mitte: die Oozyte gerade noch angeschnitten und drei Nährzellen; rechts: fünf Nährzellen, die sechste in der Mitte nur angedeutet. — Aufnahme mit Zeiss' Phoku, Negativlinse H, Objektiv × 40.

sache mit einem jüngeren Abschnitt eines normalen Ovarialfollikels von *pigra* übereinstimmen. Nach den eingehenden Untersuchungen mehrerer Forscher und besonders nach solchen von KNABEN (1934) differenzieren sich die Oogonien in die künftige Eizelle und die Nährzellen, wobei die Anzahl der letzterwähnten von der Anzahl der Teilungen bestimmt wird und zwar so, dass nach n Teilungen 1 Oozyte und 2^n—1 Nährzellen gebildet waren. KNABEN fand nämlich bei den von ihm untersuchten Arten 3, 7 und 15 Nährzellen, wobei 7 die häufigste Zahl war. Wie ich an Präparaten von *pigra*-Ovarien habe feststellen können, ist diese Zahl auch bei dieser Art die charakteristische. Es scheint mir also klar, dass die Zysten von einem einzigen Oogonium abstammen.

Wie sollen wir uns aber die Entstehung eines Oogoniums in einem

äusserlich völlig normalen Testis vorstellen? Handelt es sich um eine sonderbare Form von Intersexualität oder liegt Gynandromorphismus vor? Die Annahme einer beginnenden Intersexualität kann nach meiner Ansicht glatt abgelehnt werden. Der Fall zeigt nämlich keine Ähnlichkeit mit den von GOLDSCHMIDT in verschiedenen Abhandlungen beschriebenen und abgebildeten Fällen von Intersexualität bei *Lymantria dispar*. Hier geht die Umwandlung von den Ausführungsgängen und den in ihrer Nähe liegenden Spermatogonien aus. Diese wandeln sich allmählich in Oozyten und Nährzellen um. In unserem *pigra*-Fall setzt die Bildung von Spermatogonien fort und die Ausführungsgänge sind vollständig normal wie bei den gewöhnlichen Testes und zeigen keine Tendenz sich in Eifollikel zu verwandeln. Es scheint mir klar, dass es sich hier um einen Fall von Gynandromorphismus handelt. Auffallend und rätselhaft ist nur der vollständige Parallelismus in den beiden Testes.

Bekanntlich hat MORGAN die Entstehung der Gynandromorphen bei *Drosophila melanogaster* durch Elimination des einen X-Chromosoms erklärt. Die Gynandromorphen von *Drosophila* wären also nach MORGAN genetische Weibchen, die in einem grösseren oder kleineren Teil ihres Körpers infolge des Verlustes des einen X-Chromosoms in Männchen umgewandelt worden wären. Diese MORGANs Hypothese ist allgemein als richtig anerkannt worden. Gehen wir von dieser Hypothese aus, so können wir auch den *pigra*-Fall erklären.

Drosophila ist im weiblichen Geschlecht homogametisch, die Lepidopteren dagegen im männlichen. Zwar kann man weder beim Männchen noch beim Weibchen von *pigra* die Geschlechtschromosomen von den Autosomen unterscheiden, aber die reziproken Kreuzungen zwischen *P. anachoreta* F. und *curtula* (FEDERLEY, 1922) sowie zwischen *anachoreta* und *pigra* (unveröffentlicht) ergeben Bastarde, die klar beweisen, dass *anachoreta* im weiblichen Geschlecht heterogametisch ist, im männlichen dagegen homogametisch. Es wäre also höchst überraschend, wenn sich die naheverwandten Arten *pigra* und *curtula* anders verhielten. Wir haben also das Recht anzunehmen, dass das *pigra*-Männchen zwei X-Chromosomen besitzt, das Weibchen dagegen ein XY-Paar, das morphologisch von dem XX-Paar nicht zu unterscheiden ist. Wenn nun in einem *pigra*-Spermatogonium, das also zwei X-Chromosomen hat, während einer Mitose das eine X infolge einer Nicht-Trennung oder infolge einer Elimination der einen Tochterzelle entzogen wird, so entsteht ein Spermatogonium mit einem X-Chromosom. Dieses unterscheidet sich von dem Oogonium nur dadurch, dass es kein Y-Chromosom besitzt. Wenn aber das Y-Chromosom keine für die

Geschlechtsbestimmung wichtigen Gene enthält, so wäre das Spermatogonium in ein Oogonium verwandelt. Wir können uns weiter vorstellen, dass wenn eine solche Zelle mit einem X-Chromosom sich dreimal nacheinander teilt, so entstehen acht Zellen, von denen eine sich in eine Oozyte umwandelt, die übrigen sieben sich zu Nährzellen entwickeln, wie dies in der normalen Oogenese geschieht.

Ein Umstand, der der Nicht-Trennungs- resp. Eliminationshypothese Schwierigkeiten bietet, ist das bilaterale Auftreten der Oozyste in der *pigra*-Raupe. Ich möchte es auch nicht unerwähnt lassen, dass ich in keinem Testis der übrigen zwei *pigra*-Raupen ebenso wenig wie bei den *curtula*-Raupen oder den Raupen der Bastarde gynandromorphe Bildungen fand, trotzdem die *pigra*-Eltern der Bastarde demselben *pigra*-Stamm angehörten.

Von den beiden Annahmen, Nicht-Trennung oder Elimination, wäre ich geneigt diese als die wahrscheinlichere zu betrachten. Nicht-Trennung habe ich zwar nicht selten bei den Reifeteilungen der Spermatogenese anderer Stämme von *curtula* beobachtet, aber gerade die Testes der jetzt in Rede stehenden *pigra*-Population zeigte im Gegenteil eine sehr wenig feste Bindung der Chromosomen in der Diakinese. Dies hat zur Folge, dass die konjugierten Chromosomen sich trennen und die Metaphase-Platten der ersten Reifeteilungen eine grössere Anzahl Chromosomen als die normale haploide aufweisen. Sogar tetraploide Zahlen konnten öfter festgestellt werden, aber die Grösse der Chromosomen beweist klar, dass es sich um Univalente handelt. Selbstverständlich kann die Bindung der Chromatiden in den Spermatogoniemitosen eine andere sein als die Konjugation der maternellen und paternellen Chromosomen in der Meiosis. Aber bekanntlich sind die Chiasmata der Lepidopteren überhaupt gering an der Zahl oder können sogar ganz fehlen. Eine Elimination von Chromosomen in den Reifeteilungen ist dagegen bei Lepidopteren-Bastarden eine nicht seltene Erscheinung. Es läge also nichts unwahrscheinliches in der Annahme, dass eine Elimination auch in den Mitosen der Spermatogonien vorkommen könnte.

ZUSAMMENFASSUNG.

Es wird ein Fall beschrieben, in dem in den beiden sonst normalen Testes einer Raupe von *Pygaera pigra* in jedem eine freie Zyste mit einer jungen Oozyte und sieben Nährzellen gefunden wurde. Verf. vermutet, dass in der Mitose eines Spermatogoniums das eine X-Chromosom eliminiert oder eventuell durch Nicht-Trennung der einen Tochterzelle

beraubt worden wäre, und diese demzufolge in der Hauptsache die genotypische Konstitution eines Oogoniums erhalten und sich wie ein solches weiter entwickelt hätte.

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THE EFFECT OF CHROMOSOMAL VARIATION IN SUGAR BEETS

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INTRODUCTION.

THE sugar beet is undoubtedly one of the most intensely studied plant species owing to its great practical importance as a sugar-producing plant. All kinds of correlations between morphological and physiological qualities have been tested. Sugar beet breeding has on its program a study of especially those correlations which concern the possible connection between different exterior properties and such physiological qualities as are important for the manufacturing of sugar, as, for instance, sugar content, purity of the juice, and so on.

When the first tetraploid sugar beets were produced in 1938, an entirely new factor was added to the variation system of this plant. Nothing was known about the effect of different chromosome numbers on the properties of the sugar beet beyond the fact that other beet species with tetraploid and hexaploid chromosome numbers had been found in nature and had in certain tests shown a very high content of dry matter (VON BERG, 1935). Much interest was therefore concentrated in the question: what effect on the different properties of the sugar beet will be induced by chromosome variation, or in the terms of practical breeding: at what chromosome number will the optimal condition for sugar production be situated? Will a beet with a higher chromosome number be more accessible to improvement by current breeding methods than the diploid types? Does the doubled gene complement by any chance entail a greater tensibility in the genotype, permitting a greater number of practically important factors to be gathered by the genotype?

The enormous perspectives which are opened up by such questions make every contribution to the knowledge of the effect of different chromosome numbers in the sugar beet an object of great interest. During our attempts to produce tetraploid sugar beets (RASMUSSON and LEVAN, 1939 and unpublished) we obtained numerous triploid plants as by-products. Thus, in 1938, 319 triploids appeared per 20 tetraploid

plants, and, in 1939, 149 triploids appeared per 98 tetraploids. The triploids, which genealogically are of no value for the breeding, may nevertheless be of use for the study of beet types with different chromosome numbers, because, if they can be brought to seed setting, a great variety of chromosome numbers may be expected in their progeny. Some of the triploid sugar beets produced during 1938 were therefore crossed in greenhouse cells under artificial light in the winter of 1938—39. Progenies were taken from the triploids partly intercrossed, partly crossed with diploids. These progenies turned out to include not only all chromosome numbers between 2x and 4x but also some higher numbers. Thus they were very well suited for the study of the influence of different chromosome numbers on morphological qualities.

A reservation should be made, however, already now. The very determination of the chromosome number of each plant with the necessary replanting implies a serious hindrance for the equal and typical development of the beets. Besides, these greenhouse isolations ripened so late in the spring that the growth season on the field was considerably delayed, with the result that at the harvest the beets had not reached by far their full ripeness. I accordingly want to stress the fact that the following results must be regarded as somewhat provisional, especially as far as they concern qualities of ripeness. On the other hand, as it may take some time before the experiment is repeated, the publication of the following results appears to be well justified.

While the studies of the tetraploid sugar beets have been carried out by RASMUSSON and LEVAN, these triploid progenies have been analysed mainly by LEVAN. I wish here to express my gratitude to Dr. RASMUSSON for much helpful criticism and for the permission to use the facilities of the Hilleshög Beet Breeding Station. My thanks are also due to Dr. TEDIN for valuable help with the statistical analysis in Chapter VI: 4, and to Mrs. ANNA NORDSTRAND-LARSSON and Miss MAGNA PALM for excellent technical help.

I. THE MATERIAL.

1. ORIGIN OF THE MATERIAL.

Plants of the strains, inbred for several years, which, intercrossed, compose the commercial Hilleshög seed were treated with colchicine, so that diploid-tetraploid chimaerical inflorescences originated (the

c_0-generation). In the progeny of these plants triploid c_1-plants were selected and isolated in greenhouse cells. In all, 51 triploid plants of the strains G, P, Q, R, Y and Ä were put into six cells, while one triploid of the R strain and one diploid of the Y strain were crossed in one cell.

It may be seen from Table 1 that the quantity of seed obtained from the triploids was very much less than normally. While normal diploid plants of the same size as these triploids often give some 1000 seeds per plant, the triploids intercrossed yielded on an average only 160 seeds per plant; the triploid crossed with the diploid plant yielded somewhat more. The germination of the c_2-seeds was very poor. In one test, where 100 c_2-seeds from the triploids were compared with diploid and tetraploid c_2-seeds, no single triploid seed germinated, while 90 % of the diploids and 21—100 % of the tetraploids germinated. On an average the germination percentage of the triploid seeds was 4 %. The cross between diploid and triploid did not only give a greater quantity of seeds, but its germination was also decidedly better, 34,4 %.

All the seeds were put to germination in seed boxes on the 11th of July, 1939. They were transplanted to fixing pots as soon as they germinated. All surviving plants were fixed during the 3rd to 11th of August, and immediately after the fixing they were transplanted into the field. The first field description was made the 8th—18th of September, and their development was studied continuously during the autumn. At the harvest on the 1st of November the weight of the roots and tops was determined individually for all plants and the outlines of three leaves from each plant were drawn. Small pieces of the leaves were fixed for subsequent study of the stomata and plastids. All sufficiently big roots were sampled for the refractometer test.

During the winter of 1939—40 62 of the harvested roots were planted in the greenhouse. This material included representatives of several somatic numbers and was intended for a study of their morphology, for fixing of meiosis, and for crossings.

2. CHROMOSOME NUMBERS OF THE MATERIAL.

Table 1 gives a survey of the different somatic chromosome numbers found in 130 plants of the diploid-triploid crosses and in 368 plants of the triploid-triploid crosses. As is seen, all numbers between 18 and 38 occur and, in addition, the numbers 42, 44 and 45 (the latter = 5x).

TABLE 1. *Origin of the material and its chromosome numbers.*

| Field number 1939 | Type of cross | Number of parental plants | Number of seeds | Germination % | Total of surviving plants | Somatic chromosome number | | |

sented by 5 %, while trisomics and 20-chromosome plants have 13 % and 18 % respectively, the latter percentage being the maximum for the entire curve. A minimum is situated between 2x and 3x, and the plants which survive within this region are often abnormal and poor. Nevertheless, 10 % of the progenies are found between the classes 22 and 25, and no class, not even the very inferior class of 23, has less than 11 plants. This fact confers a great advantage on the present material as compared with other materials in which the effect of the chromosome numbers on the external morphology of the plants has been studied. The region above the triploid number has, it is true, often been very well-represented, but in few earlier cases has the region between 2x and 3x been so completely represented as in the present case. And, since the effect of each single chromosome must be greater in this region than in the region above 3x, special interest attaches to the aneuploid numbers between 2x and 3x. The mode at 3x is not very pronounced, the 3x class being represented by 7,3 %. Whether there really is a shallow minimum between 3x and 4x, cannot be decided with certainty. The classes 30—35 are rather well represented and include 21,7 % of the curve. Above these classes the curve falls definitively, and the classes above 34 have only single plants, 35—37 having together 1,8 %. The chromosome numbers above 4x include four plants and may be interpreted as the result of unreduced gametes.

II. THE VIGOUR OF THE DIFFERENT CHROMOSOME CLASSES.

Even at the germination of the seeds very decided differences in vigour were already apparent between the young seedlings. Some grew rapidly into normal plants, others developed very slowly and assumed a distorted and abnormal appearance. The field plots exhibited a great diversity of normal and anomalous plants. It could be early observed that No. 18108 (2x × 3x) differed from all other numbers in having a preponderant number of normal and well-delevoped plants. This number turned out to contain 77 % of diploids.

A number of properties connected with the vigour of the plants were noted individually in each of the about 500 plants in the field, partly on different occasions during the vegetation period, partly at the harvest in November. Since the different numbers were all treated as far as possible in the same manner, the values obtained for the different progenies can be combined. In the triploid progenies only

two 4x-plants were present, so in certain cases I also used the values from a material of tetraploids consisting of three numbers with in all 65 plants, which were treated in the same manner as the triploid progenies. All values collected in the field and afterwards have been calculated as mean values for each chromosome number. They are given in Table 2, in which columns 3—18 deal with such qualities as more or less directly give a picture of the plant vigour. In the present chapter the following points will be discussed: estimation of general vigour in the field, percentage abnormal and deformed plants, weight of tops and roots, refractometer determination, and some leaf characters.

1. FIELD ESTIMATION.

The field estimation was carried out in the middle of September. Each plant was given a score from 0 to 10. A diploid plot, treated exactly as the triploid progenies, was used as a standard for the score 5 of the scale. The third column of Table 2 gives a survey of the results. A very characteristic phenomenon, which is also present in the other vitality curves, is immediately seen, viz. an obvious trimodality. The 2x class has a rather high average, 7,9, thus somewhat higher than the diploids of the standard plot. This increase in vigour is obviously caused by the condition that the diploids in the triploid progenies were usually surrounded by small dwarfed plants and consequently could develop without competition. The curve falls rapidly from 18—19 and reaches its minimum at 22. Between the classes 22 and 23 the middle point is situated between 2x and 3x, which implies a maximal chromosomal disharmony of these classes. Here the curve turns and then goes rapidly upwards to 3x, which class is somewhat superior to the standard beets but inferior to the 2x of the triploid progenies. Between 3x and 4x there is another minimum, though a decidedly less deep one. The bottom point is at $2n = 34$, which has an average score of 3,6. 4x constitutes the third mode, rising above the classes on both sides. Its score (5,3) is computed also from the 65 extra plants and consequently the value must be considered rather reliable. Evidently within this material there is a gradual decrease in vigour from 2x over 3x to 4x.

At the same time as this estimation was carried out it was also noted whether each plant had a normal appearance or was in one way or other malformed. The score was intended only as a measure of the general development of the plant, and it was soon realized that

considerable differences were present between normal and abnormal plants at the same developmental stage. All kinds of abnormalities were met with, some of them being indicated in Fig. 1. The shape of the leaves could be extremely narrow, often with folded and torn edge. Frequently the harmony between lamina and vascular tissue seemed to be disturbed, so that the lamina had to fold and buckle in order to get room between the nerves. This could result in a regular corrugation, especially evident in that part of the leaf which runs down on the petiole. The thickness of the leaf was often abnormally great. This condition, however, may be ascribed to the severe draught (the same symptoms as those of the »jaunisse» disease). In extreme cases the leaves were subulate and at the same time they were extremely brittle. Their colour also varied, the same appearance as in mosaic disease was common, and also purely yellow plants were found. These abnormalities are no doubt caused by the disturbed chromosomal balance, which is made especially clear in the trisomics, where the habitual abnormalities could be grouped into certain types (see Chapter IV). That the unbalanced types contain a greater proportion of malformed plants is seen from column 4 of Table 2. A maximal frequency of abnormal plants is recorded in the classes between 2x and 3x in classes 21—23, considerably more than half of the plants being clearly abnormal, while the frequency of normal plants increases towards both 2x and 3x. From class 26 and upwards abnormal plants are rare, averaging 3,9 %. In detail these abnormal plants were found in the following classes: 4 in class 28, 2 in class 32, 1 in each of the classes 30, 31, 33 and 34. Thus, it may be concluded that when the chromosome number increases to above 3x the plants are able to resist the chromosomal unbalance in quite another manner than when the number is below 3x.

Two 18-chromosome plants, or 3,1 % of the diploids present, were clearly misformed. A leaf from one of them is pictured in Fig. 1 *a*, the last leaf of the first row. It is easily understandable that the chromosome number *per se* is no guaranty of a complete and balanced gene complement. It is true that even among inbred diploid sugar beets similar abnormal plants may be met with as segregation products. In these triploid progenies, however, it is more likely a question of structural chromosomal aberrants, originated during the triploid meiosis and concealed under a normal chromosome number. One indisputable case of structural hybridity in an 18-chromosome sugar beet among the triploid progenies is recorded in Chapter V: 2.

TABLE 2. *The correlation between chromosome number and various qualities.*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
							Refractometer determination		Leaf characters									Stomata				Plastids			
													Laminæ												
															Index										
Somatic chromosome number	Total number of plants	Field estimation	% abnormal plants	% lethality	Weight of tops	Weight of roots	Number of plants	Mean values	Total number of leaves	Number of small leaves	Number of plants with many small leaves	Length of petioles	Length	Breadth	Large	Medium	Small	Studied number	Mean length	Smallest mean	Greatest mean	Studied number	Mean size	Smallest mean	Greatest mean
18	64	7,9	3,1	3,1	137	81,6	58	24,1	22,3	9,2	4	10,2	160,4	108,7	1,5	1,9	2,0	21	28,8	24,2	34,0	19	5,78	4,29	7,13
19	70	4,6	12,9	10,0	72	30,8	46	26,3	20,1	10,5	13	8,4	133,4	90,2	1,5	1,9	2,2	37	31,6	21,1	36,7	16	5,90	3,50	7,97
20	90	3,4	38,9	8,9	35	16,0	22	27,4	19,0	9,3	18	6,3	111,3	66,1	1,7	2,2	2,2	23	33,3	27,2	40,9	21	6,27	4,02	11,23
21	34	3,0	64,7	5,9	30	11,6	9	24,6	18,2	9,9	4	6,3	98,3	51,2	1,9	2,2	2,5	5	35,0	29,8	40,6	3	5,43	4,18	7,69
22	11	2,5	63,6	0,0	18	8,0	4	24,3	14,0	6,5	1	5,2	93,0	44,0	2,1	2,6	2,5	2	37,9	30,6	45,2	2	6,79	5,03	8,46
23	13	2,7	61,5	7,7	19	5,8	1	22,5	15,0	7,1	1	4,8	88,3	54,2	1,6	2,1	2,1	5	36,7	33,7	43,6	1	5,54	—	—
24	15	2,6	26,6	6,7	24	10,0	3	26,8	11,8	9,0	1	5,2	91,9	54,2	1,7	2,3	2,7	5	33,7	30,2	42,2	0	—	—	—
25	12	3,7	16,7	8,3	45	17,7	5	25,9	16,6	10,3	2	7,3	148,0	80,0	1,9	2,1	2,2	5	33,9	26,3	44,8	1	5,10	—	—
26	25	4,6	↑	12,0	66	28,8	16	25,7	16,6	7,3	—	6,4	136,8	89,3	1,5	2,1	2,2	5	37,6	29,1	42,3	2	6,12	5,74	6,83
27	30	6,3		↑	136	68,3	25	24,2	18,8	8,2	1	8,3	159,5	115,0	1,4	1,9	2,0	20	36,2	28,9	49,4	16	6,23	3,67	7,84
28	21	4,6			89	46,9	14	24,3	17,8	9,2	1	7,4	148,8	96,4	1,5	1,9	2,0	5	41,1	36,7	47,0	1	5,50	—	—
29	11	5,1			76	37,0	9	26,2	16,0	7,0	—	6,5	152,0	96,0	1,6	1,9	1,8	5	39,0	36,6	45,2	2	6,72	6,78	7,79
30	24	4,0			63	22,8	15	26,1	15,9	7,1	—	5,9	128,2	86,4	1,5	1,9	2,0	5	36,0	31,7	41,8	5	6,49	5,44	6,54
31	15	4,5	3,9		63	26,3	12	26,9	15,5	6,9	1	6,9	139,7	87,9	1,6	2,0	2,1	5	37,1	31,8	44,0	2	5,91	5,33	6,62
32	20	3,9		6,7	46	22,8	12	26,4	15,5	6,1	—	6,0	128,3	78,3	1,6	2,1	2,1	5	38,2	29,4	48,6	2	7,14	5,81	8,18
33	21	3,8			57	26,6	12	25,1	16,9	9,1	2	6,3	128,2	83,4	1,5	1,9	2,1	5	43,4	38,4	52,4	0	—	—	—
34	11	3,6			63	29,5	7	26,2	15,3	6,6	—	6,2	128,6	94,1	1,4	1,6	1,7	5	43,2	39,0	52,6	3	8,67	7,36	11,03
35	2	4,7			101	50,0	2	24,5	15,0	7,5	—	5,0	160,0	110,0	1,5	1,6	2,0	4	40,0	34,9	41,6	2	7,67	6,90	8,96
36	2	5,3			126	65,0	2	24,5	15,0	7,5	—	8,5	185,0	125,0	1,5	1,7	1,9	29	37,4	31,0	43,5	28	5,67	3,91	7,67
> 36	7	3,9	↓	↓	112	62,1	6	25,5	17,5	6,7	—	6,7	166,7	123,3	1,4	1,8	2,3	11	41,0	30,2	50,3	7	6,44	4,52	8,64

In connection with the field estimation in September a list was made of those plants which had died after the transplanting into the field. Their chromosome numbers were known, and they were distributed over the different classes according to column 5 (Table 2). In these cases it is more difficult to see any regularity in the numbers; it seems that merely casual external influences have played a greater rôle than the chromosome constitution. The trisomics had a great mortality (10 %), while classes 20—25 had a lower mortality, — in reality, no plant of class 25 had died. It may be that the greatest strain on the vitality of these classes is effected earlier, for instance, at the germination, so that the plants which really germinate are able to keep alive, although often very languishingly.

2. WEIGHT OF TOPS AND ROOTS.

Columns 6 and 7 of Table 2 show the weight of tops and roots at the harvest. As already pointed out, the growing period of these beets was very much shorter than usual, being only about 3 $^1/_2$ months as against the normal 5 months. Owing to this the absolute values of top weight and root weight have little significance. Thus only two beets of the entire material had a root weight of 200 gm., while the mean root weight of normal beets in the same field was about 400 gm. Nevertheless, the relation between the weights of the different chromosome classes is of great interest, as the root weight may be considered a a measure of the sum production capacity of the plant, provided no great differences in dry matter percentage occur within the material.

The curves of top weight and root weight agree, as could be expected, both with each other and with the field estimation curve. They have maxima at 2x, 3x and 4x, and between these classes there are minima, the one between 2x and 3x decidedly deeper than the one between 3x and 4x. 2x has the highest value in both curves, but the two modes of the top weight at 3x and 4x are only a little lower (the three values being 137, 136, 126 respectively), while the greatest decrease in root weight is from 82 of the diploid to 68 of the triploid, while the tetraploids have a mean weight of 65. The courses of the curves are similar even in detail, depending on the relation between top and root weight being rather equal even in beets of different size. This relation in the present material may be expressed thus, that the root weight was on an average 45,7 % of the top weight. This percentage varied from class to class, being lowest in class 23 with 30,5 %, and

TABLE 2. *The correlation between chromosome*

highest in class 18 with 59,6 %. A certain trend in this variation was evident: class 18 was above the average, classes 19—26 were all below the average (class 20 = the mean, though), classes 27—29 above, 30—

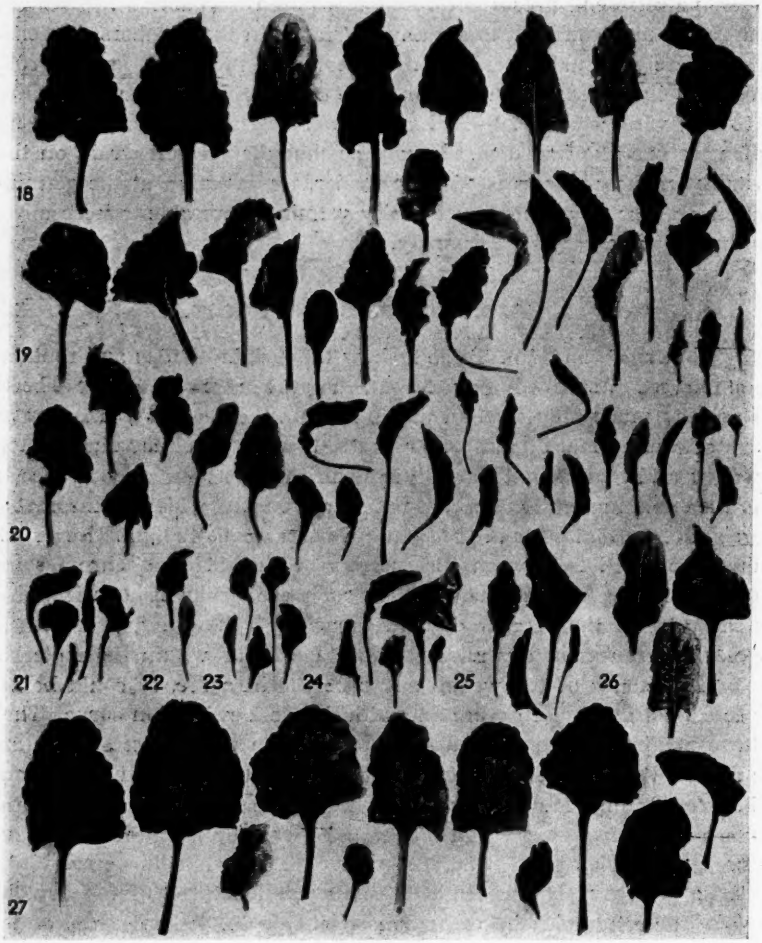

Fig. 1 *a*.

31 below, and all classes over 31 were above the average. This relation follows, as may be seen, the viability curve in general and is due to the condition that in more well-developed beets the roots constitute a

greater part of the total plant than in weaker plants. This weight relation of tops and roots again stresses the condition already pointed out several times, viz. the poor ripeness of this material at the harvest.

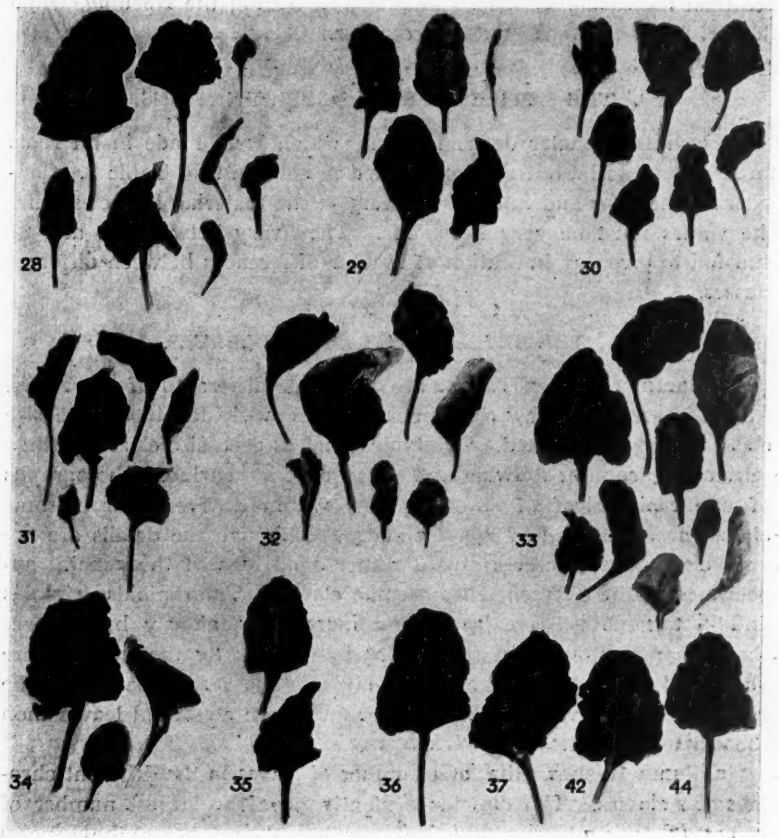

Fig. 1 *b*.

Fig. 1 *a*, *b*. One well-developed and typical leaf from each of the plants of No. 18112. The leaves from plants with the same somatic number are grouped together, the 2n-number being given below to the left of each group. It may be seen from the pictures that the euploid numbers 18, 27 and 36 are characterized by larger and more harmoniously developed leaves than the intermediate numbers. The decrease in viability is more pronounced between 2x and 3x than between 3x and 4x.

As is well known (compare, for instance, RASMUSSON, 1936) the tops and the roots of normal beets during their maturation run through

the following relations: the top weight in the first part of the season is higher than the root weight, some time during August—September, however, the root weight reaches and passes the top weight. The roots are then increasing in weight all the time during the ripening, while the weight of the tops gradually diminishes.

3. THE REFRACTOMETER DETERMINATIONS.

The refractometer determinations, which were made in all roots large enough to be tested, are collected in column 9 of Table 2. Considering the poor and unequal ripening of the material, it is clear that the values must be very unreliable. They vary between 22 and 27 and fail to give any indication of regular differences between different classes.

4. THE DEVELOPMENT OF THE LEAVES.

Columns 10—18 of Table 2 are devoted to different leaf characters. At the harvest the leaves of each plant were divided into three size classes and were counted. One typical leaf of each size class was then selected for contour-drawing and subsequent measuring. Photographs of one typical leaf of several plants within different chromosome classes are submitted in Fig. 1 *a* and *b*. Although the details are not very clear, these pictures give a rather good idea of the general appearance of the different chromosome classes. The diploids, triploids and ± tetraploids have larger and more harmoniously built leaves than the aneuploids. In the photograph especially the triploids are characterized by large and broad leaves. It is readily seen that the classes 20—25 have decidedly smaller and more abnormal leaves than the classes 29—34.

Column 10 shows the total number of leaves in the different chromosome classes. The diploids evidently have the largest number of leaves (22 per plant). The leaf number then follows the general viability curve, forming a minimum at the classes 22—24 and a mode at 3x. It falls again above 3x, and whether it forms a new mode at 4x cannot be decided, since the few variates of the higher classes are scattered rather irregularly. The numbers of the smallest leaves (col. 11) make a rather irregular curve. It has a slowly falling tendency but lacks the maxima and minima of the total curve. It may be concluded that just the weaker chromosome classes, in which the total leaf number is lower, strive to compensate their weakness by forming

new leaves, while in the more vigorous classes 2x and 3x a greater proportion of the total leaf number consists of full-grown, ripe leaves.

Even in the field I noticed a characteristic type of tops, sometimes also found among diploid material, but occurring here in a much greater frequency, viz. a top consisting of a few large, well-developed leaves plus a whole tuft of small, often malformed leaves in the centre. As I had a decided impression that this type was a sign of lacking vigour, especially since sugar beets are known to respond with the same peculiarity of the top towards certain diseases, I decided to investigate whether this top was found more frequently in certain chromosome classes than in others. I made a record of all beets bearing more than 20 leaves of which more than half were small. As an instance of the types sought, the following five beets may be mentioned, constituting the plants of this kind found in number 10814: 6 large + + 7 medium + 16 small leaves = total 29 leaves; 7 + 8 + 16 = 31; 6 + 8 + 35 = 49; 7 + 5 + 13 = 25; 6 + 8 + 15 = 29. In the entire material 49 beets of this type were found. They are collected in column 12 of Table 2. Although they are distributed over most of the chromosome classes, it is evident that the classes between 2x and 3x have the majority of these plants. 40 such plants out of 270 occur in these classes, while the other classes, with a total number of 228 plants, only have 9 plants of this type.

The length of the petioles of the large leaves (Table 2, column 13) is a property which on the whole follows the vigour curve. The diploids have the largest petioles, 3x and 4x form modes with somewhat lower values than 2x. The fall from 2x down to 19—23 is very clear, and so is the increase in length towards 3x. Above this number the curve is more irregular. It may be concluded that the correlation between chromosome number and length of the petioles is rather loose.

After the production of the first tetraploid beets we already made (RASMUSSON and LEVAN, 1939) the observation that the tetraploids had larger breadth of their leaves in relation to the length than the diploids. It is therefore of great interest to check the behaviour of these two factors along the whole series of chromosome numbers. In Table 2, columns 14 and 15 the mean length and breadth of the largest leaves are given, and in columns 16—19 the length : breadth indices of the three size classes of leaves are tabulated.

As could be expected, the curves of length and breadth of the leaves show, broadly speaking, a corresponding course. They follow the general vigour curve, forming modes at 2x, 3x and 4x, a deep minimum

between 2x and 3x, and a shallow minimum between 3x and 4x. A very characteristic feature of the curves is that they diverge in the less vigorous classes, i. e. the leaves of these classes are longer and narrower. This is clearly seen in the indices of column 16. Especially between 2x and 3x the index springs up. On the other hand, in this material there is no difference between the indices of 2x, 3x and 4x, as perhaps should have been expected, especially as the general impression of various polyploid materials is that they have relatively broader leaves than the corresponding diploids. PETO and BOYES (1940), however, found no such change in the length-breadth relation in their triploid beets. As already stressed, no general conclusions can be drawn from my material, since in several respects it developed under unfavourable conditions.

The index of medium and small leaves is also calculated (columns 17 and 18). The curves for these leaves have the same general tendency as that for the largest leaves; the variations of the curves are less regular, however, especially of the curve for the smallest leaves. The average of the indices is greatest for the smallest leaves, and *vice versa*. In number 18112 I investigated this condition in some detail. It turned out that of the 176 plants of this number 43 % behaved in this manner. If this normal sequence of indices is designated 123, the result of the analysis may be arranged in the following way:

Sequence of indices	123	132	213	231	312	321	Total of plants
%	44,9	25,6	12,5	10,8	2,3	3,9	176

No special chromosome class deviated with certainty from the rest in this respect. These conditions are evidently an expression of a biological phenomenon, viz. growth in length is more rapid in the beginning, while growth in breadth predominates later on.

5. SUMMARY OF THE VIABILITY RELATIONS WITHIN THE FIELD MATERIAL.

Before leaving the chapter on the relative vigour of the different chromosome classes, I shall consider the material from another angle, viz. a comparison of the three different types of crosses which were present: diploid × triploid, triploid × diploid and triploid × triploid

(Table 3). This is of course just a re-arrangement of the preceding results, since the somatic numbers present within the progenies of the different types of crosses are absolutely decisive for their phenotypic appearance. On the other hand, this mode of approach gives a better picture of the situation in the field than do the class values.

No. 18108, which is a 2x × 3x cross, differs strikingly from the other numbers, with a far better viability. This can be seen from all different qualities, and was, as earlier mentioned, also apparent in the field. The two last columns of Table 3 give the reason for this, the percentage of diploids being very much greater and the percentage of

TABLE 3. *Means of the different types of crosses.*

Field number	Number of plants	Type of cross	Field estimation	Weight of tops	Weight of roots	Number of leaves	Length of the largest leaf	Breadth of the largest leaf	Index of the largest leaf	Percentage of diploids	Percentage of aneuploids between 2x and 3x
18108 ...	53	2x × 3x	7,7	120,5	68,6	18,8	151,5	101,2	1,5	77,1	18,9
18107 ...	82	3x × 2x	4,9	54,4	23,3	15,8	117,9	71,6	1,7	9,8	89,0
18111—18116 ...	391	3x × 3x	4,9	64,4	28,6	16,2	129,9	81,7	1,6	5,2	51,1

aneuploids between 2x and 3x being smaller than in the other types of crosses.

The crosses triploid × triploid are less vigorous but constitute a transitional stage, since they are somewhat more vigorous than the 3x × 2x cross. This is true in spite of the fact that they contain fewer diploids than the 3x × 2x progeny. Their mean vigour is increased, however, by the presence of the classes above 3x, which are not present in the 3x × 2x progeny.

From the table it will be seen that the breadth of the leaves both absolutely and relatively is greatest in the 2x × 3x progeny. This accords with the low frequency of aneuploids between 2x and 3x in this progeny. As earlier pointed out, especially these classes tend to increase the leaf index.

III. PROPERTIES OF THE CELLS.

It is a well known fact that the cell size increases with increasing chromosome number. This condition is of great use in the picking out of experimentally doubled forms. The cells usually employed for this

purpose are stomata and pollen grains. This size relation of diploid and tetraploid cells has, it is true, been studied very often; the intermediate classes on the other hand have seldom been measured. I therefore considered it worth while to use the present beet material with its complete assortment of chromosome numbers for such measurements.

Of each plant, 20 stomata were measured, and in each chromosome class usually five plants were studied. Of the classes 2x, 2x + 1, 2x + 2, 3x and 4x, however, about 25 plants were measured (Table 2, column 19). The means of these measurements together with the limits of variation of the plant-means are tabulated in Table 2, columns 20—22. From these values it is seen that an increasing tendency is evident within the whole curve, although the single mean values vary a great deal. There is a risk of getting single plants among the diploids with a cell size well within the variation area of the tetraploids. This is in agreement with the experiences from the pollen measurements. Although pollen measurements in beets are of an indispensable help in recognising tetraploid plants, branches or single flowers, the results are not unquestionable. Now and again diploid plants are found with as large or larger pollen than the average tetraploids. The genic variation works in such cases in opposition to the genomic variation.

On a closer study of the stoma length of the different chromosome classes, it becomes evident that the increase in size is more rapid in the first part of the curve. Above 3x the increase gradually diminishes, and when 4x is passed it very probably tends to become asymptotic. A stray value from a hexaploid sugar beet recently produced supports this view. The hexaploid had a stoma length of 43 μ, thus not greater than in classes 33—36 of the present investigation. It would be interesting to compare the site of the viability optimum and the course of the cell-size curve. This much seems to be sure: when the curve enters its asymptotic stage and consequently the plant cell ceases to respond with an increase of volume to an increase in chromosome number, the optimum of vigour will soon be passed, since purely mechanical troubles of the chromosomes must originate. This situation is present after prolonged colchicine treatments, and the mitotic disturbances caused by chromosome crowding can be directly observed in such material.

A quality which is very little known is the dependence of the plastid size on the chromosome number. In order to study this quality

in the beet material, pieces of leaves were sectioned and the plastids of palisade cells from the same layer and from comparable parts of the leaf were measured. Although rather comprehensive data were collected in this way, the results were entirely negative. The mean values of 50 grains in each plant and several plants in each class are collected in Table 2, column 24, the variation limits of the means being given in columns 25—26. These values show no definite differences between any classes. And a still greater material of diploids and tetraploids which was investigated by RASMUSSON and LEVAN (unpublished) also failed to demonstrate any difference between the plastid size in diploids and tetraploids.

During the study of meiosis the size of the nucleolus at exactly similar diakinesis stages was measured several times. It turned out that the nucleoli of high chromosome types were decidedly larger than in the diploids. Only few measurements were made, it is true, but since they all point in the same direction I am submitting them below:

2x: 1,8μ
2x + 1: 1,6μ, 1,8μ
3x: 1,9μ, 2,1μ
4x: 2,5μ
4x + 6: 2,5μ

IV. THE TRISOMIC CLASS.

Among the different somatic numbers the trisomics deserve special attention, since they afford a means of studying the action of each of the nine chromosomes of the genome when present three times. As many as 62 trisomic plants survived in the field. In the middle of October, when their development had become maximal, I made a thorough revision of them, systematically recording a number of their qualities. I found them to vary quite considerably. On describing their variation I first directed my attention to their general type, whether erect or prostrate, whether normal or in any way malformed. After that the shape of the leaves was recorded, and great significance was attributed to the relation between length and breadth. Also the general viability of the plant was considered important. Only in the second place were such qualities noted as leaf colour, glossiness, curledness, crispness of the leaf edge, and so on, which are all qualities easily affected modificatively.

In all there was found among the trisomics 41 clearly erect plants, 10 semiprostrate and 11 prostrate ones. If the leaf types were roughly divided into broad and narrow types, there occurred 24 broad and 17 narrow types among the erect plants, and 4 broad and 6 narrow among the semiprostrate, while all prostrate plants had broad leaves. A division according to vigour showed that among the erect with broad leaves 20 plants had superior or medium vigour and 4 had bad vigour, among the erect narrow-leaved plants 8 had good vigour, while 9 were more or less poor. Among the semiprostrate only one plant was of an inferior viability, while all the 11 prostrate plants had an excellent vigour. The leaf colour was distributed unequally on erect and prostrate plants. The former were predominatingly light types (25 among 41), the semiprostrate had 3 light plants contra 7 dark, and the prostrate were all dark-green.

It soon became evident that certain characteristic types were repeated in the material. These types had, it is true, a similar appearance as may be found in any beet field, but the qualities which characterized the different types were often exaggerated far beyond the variation limits of ordinary diploid sugar beets. The stability of these types will be tested later on by an individual propagation of each trisomic type. For the present I shall limit myself to a brief mention of five of the most characteristic types, well aware that this classification must so far be very provisional.

1. *The »glass-type»*. — Erect, leaves broad, oblong-ovoid, thick, brittle, »glassy», surface smooth or fine-buckled, colour glossily green, edge smooth or fine-erose, petioles short, vigour rather good (4—7).

This type is characterized by its thick glasslike leaves; five plants belong to this class.

2. *The »lettuce-type»*. — Erect, leaves ovoid, broadly rounded, thin, surface coarsily buckled, colour light-green, nerves white, edge smooth, petioles short, vigour very good (6—9).

A very characteristic type, same habit as garden-lettuce; three plants (probably 6) of this type have been identified.

3. *The »mosaic-type»*. — Erect, leaves broadly ovoid to triangular, thin or half-thick, surface extremely fine-buckled, colour light, often mottled (deficient of chlorophyll), edge smooth or erose, vigour poor or medium (3—6).

Easily recognizable by its fine-buckled, mosaic-coloured leaves. The meiosis of one of these plants was studied and the extra chromosome turned out to be one of the largest chromosomes, which should

be considered in connection with the poor vigour of this type. Five plants have been met with.

4. *The »horseradish-type»*. — Semi-erect, leaves long, channel-formed, of normal thickness, surface smooth, glossy, colour dark-green, often anthocyanin, edge fine-erose often crispy, petioles short with down-running lamina, this part of the lamina transverse-folded, vigour good (5—7).

Very characteristic with its long channel-shaped, glossy leaves. Eight plants of this type were recognized. Meiosis was studied in one of them, and it was demonstrated that the nucleolar chromosome was present as the extra chromosome.

5. *The »bullate-type»*. — Prostrate, leaves broad, short, triangular, of considerable thickness and often leathery consistency, surface extremely transverse-furrowed, colour dark- or grey-green, dull, edge smooth or coarsly erose, long, often white petioles, vigour very good (6—9).

This is the most striking among the trisomic types and the most vigorous one, easily recognizable on its short cross-folded, bullate lamina. Evidently the extra chromosome has favoured the longitudinal growth of the lamina, without favouring the growth of the nerves, this having given rise to the extreme transverse folding. Nine plants belong here.

In the rest of the material, which has not been included in any of the above-mentioned types, I was often able to discern two or three plants with a striking external resemblance. Still, I have not ventured either to make a new type of them or to assign them to any of the types proposed above. In order to identify the remaining four primary trisomics, it will be necessary to study a richer material.

V. CYTOLOGICAL INVESTIGATIONS.

The diploid chromosome number of the sugar beet is 18. Its somatic chromosomes are pictured by RASMUSSON and LEVAN (1939, Fig. 3 *a*). It may be seen from this picture that the chromosomes are rather small, the largest chromosomes having a length of 3 μ with a breadth of $^1/_4$ μ. Size differences within the idiogram are trifling, the smallest chromosomes being very well 2 μ in length. Sixteen of the chromosomes are medially inserted, while two of the medium-sized chromosomes have clearly submedian centromeres, dividing the chromosomes in the ratio of 2 : 1. The shorter arm of this pair has a

small satellite, which, however, is rarely visible, and this arm is connected with the nucleolus. The idiogram of the sugar beet is thus not very well-suited for studies involving the identification of single chromosomes. In fact, only the nucleolar chromosome is recognizable and this only at certain stages. Fortunately this chromosome is especially evident at late diakinesis, the nucleus being large at this stage and the chromosomes strongly contracted, with the result that the nucleolar chromosomes often lie separated from the rest of the chromosomes. Among the other chromosomes it is possible only to decide whether a particular chromosome belongs to the larger or the smaller in the idiogram.

In spite of the unsuitability of the material for cytological work, I was not contented with the mere determination of the somatic chromosome numbers. As already mentioned, I planted a collection of the harvested roots in the greenhouse during the winter of 1939—40. Most of them shot flower stalks, and meiosis was fixed. The following types were fixed: 9 diploids, 20 trisomics, 2 20-chromosome plants, 8 triploids, 2 tetraploids, 1 with 42 and 1 with 45 chromosomes. In about half of the fixations good slides of metaphase I were secured. In the present paper meiosis is described in some of the types characteristic of triploid progenies. Normal diploids and tetraploids are excepted, however, since their meiosis will be described by RASMUSSON and LEVAN.

1. THE TRIPLOIDS.

One triploid plant of the c_1-generation was fixed, viz. 10 *a* of the Y strain. It did not participate in those crosses which are dealt with in the present paper, but it was a sister plant of these triploids. Further, I investigated 5 c_2-plants: 18107—49, 18108—11, 18112—22, —30 and —37. They were all tall, vigorous plants which flowered richly.

Diakinesis is the first stage of meiosis approachable for study, earlier stages are not clear. At diakinesis the chromosomes of the triploids are present as trivalents. Often nine trivalents may be counted in the cells. Most chiasmata are completely terminalized at late diakinesis, but interstitial chiasmata are also found. Fig. 2 *a—l* pictures a number of diakinesis-trivalents. A characteristic feature is that the three chromosomes of each trivalent seem to lie at some distance from each other, their position and sometimes thin connecting fibres show, however, that they are associated. The most common trivalent type is the chain trivalent, but not so seldom also the ring-

and-rod trivalent may be seen (Fig. 2 *a*, *b*, *g*). The nucleolar trivalent (Fig. 2 *i*—*l*) is very characteristic. It is evidently the asymmetric chromosome, the shorter arm of which is attached to the nucleolus. Sometimes all three nucleolar chromosomes are gathered closely together, sometimes two chromosomes are situated at one side of the nucleolus and the third chromosome at the opposite side.

When the nuclear membrane disappears, the chromosomes become

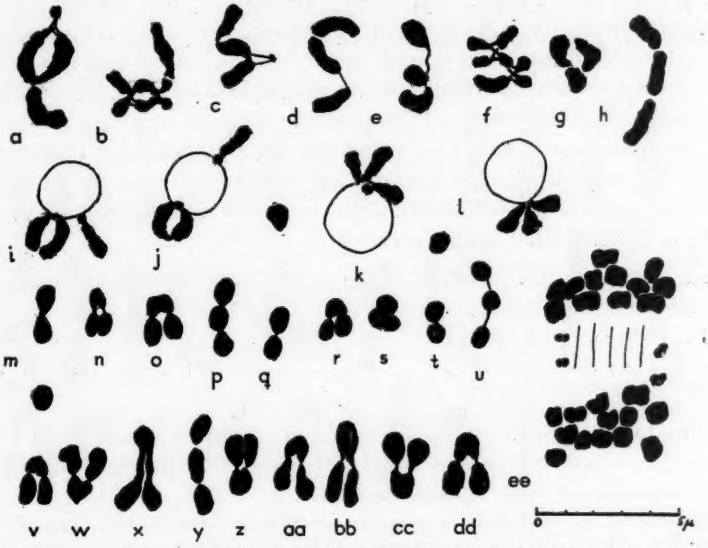

Fig. 2. Meiosis of the triploid, *a*—*l*: diakinesis trivalents, *m*—*u* and *v*—*dd*: 2 analysed metaphase I plates, *ee*: anaphase I. — × 2400.

still more contracted, although in a very different degree in different plants. In good fixations it is now easy to analyse whole cells and count the different chromosome configurations. In one plant, 18112—99, the following frequency of different associations was recorded:

9_{III}	$8_{III}+1_{II}+1_{I}$	$7_{III}+2_{II}+2_{I}$	$6_{III}+3_{II}+3_{I}$	$5_{III}+4_{II}+4_{I}$	$4_{III}+5_{II}+5_{I}$	Total
15	27	20	6	3	1	72

Fig. 2 *m*—*u* and *v*—*dd* show two analysed metaphase plates with $6_{III}+$ $+3_{II}+3_{I}$ and 9_{III} respectively. As seen from the picture, chain trivalents are the commonest; they can be straight or bent in the middle

chromosome. Ring-and-rod trivalents, and more rarely three rods joined at one point, have also been met with.

The anaphase takes place rather regularly. It is often noticed, however, that univalents proceed to the equator and are afterwards divided. Fig. 2 *ee* shows such a division at which two univalents have been divided. These univalents seem to have a stainability different from the rest of the chromosomes, they appear extremely small, and are stained very faintly. On a few occasions I have noticed typical bridges between the poles at the triploid anaphase, which indicates that more profound disturbances may occur. In the next paragraph it will be shown how one individual among the triploid progeny has obtained a structural change in its chromosomes. This stresses the lability of the triploid meiosis and shows that the triploids may be a source of structural as well as numerical changes within the species. The chromosome number of some first anaphase groups was determined in one slide. The following counts resulted:

Number of chromosomes	10	11	12	13	14	15	16	Total
Number of cases ...	3	3	2	6	4	1	1	20

As would be expected, the classes 13 and 14 are most numerous. The telophase I and the second division are regular. Solitary vagabonds and micronuclei may be seen, however.

2. A STRUCTURAL HYBRID AMONG THE DIPLOIDS.

The following diploids were studied: 18107—10, —23, 18108—32, —33, 18112—7, —48, —191. They were normal, vigorous plants, their field estimation score ranging from 6 to 10. All except one showed a perfectly regular meiosis. The abnormal plant, 18107—23, originated in the 3x × 2x cross. It had a normal appearance in the field (score 9) with 15 leaves, both tops and root weighed considerably above the average. Its somatic chromosome number 18 was checked twice. Since the viability was so very good, the cytological changes can *a priori* scarcely be ascribed to the addition or the loss of any considerable chromosome portion; instead, they must rather be sought among intra-genomic changes.

At metaphase I (Fig. 3) nine bivalents were sometimes formed. Then, however, two clear heterobivalents were most commonly visible.

Fig. 3 *a—i* pictures one such plate, where *b* and *c* constitute the two heterobivalents. Especially one of them was striking (*c*). One of its components was very much larger than the other and also larger than any beet chromosome, both in length and breadth. Four instances of this heterobivalent are illustrated in Fig. 3 *j—m*. Within the smaller heterobivalent the size difference between its two component chromosomes was less pronounced and was observed only in favourable cases. Its two chromosomes were of about the same size as the smaller chromosome of the larger heterobivalent.

Often a trivalent was seen in this plant, and then a univalent was

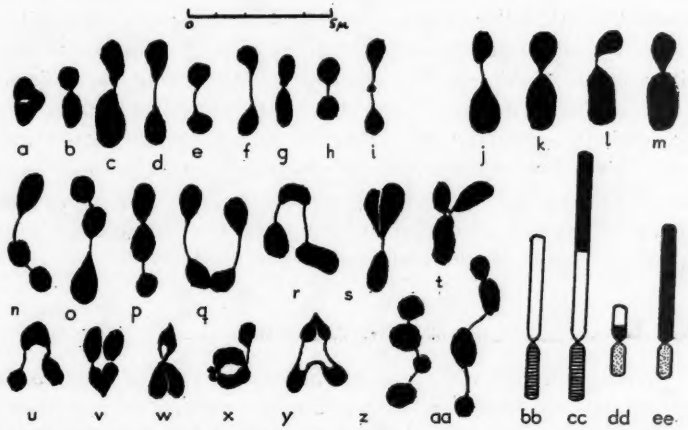

Fig. 3. Meiosis of a diploid interchange heterozygote, *a—i*: an analysed metaphase I plate, *b* and *c* are the heterobivalents, *j—m*: instances of the large heterobivalent, *n—aa*: different types of associations of 3 and 4 chromosomes, *bb—ee*: a scheme showing the possible nature of the interchange. — × 2400.

invariably present in addition. The chromosomes of the trivalent were either clearly of different size (Fig. 3 *n—t*), one chromosome being much larger than the other two, or they were of a more equal size (Fig. 3 *u—y*), the trivalent then being smaller. In the former case the trivalent could form a chain (Fig. 3 *n—r*) or a Y-trivalent (*s—t*). In the chain the large chromosome was situated proximally or distally. Also the smaller trivalent usually formed a chain, most often bent in the middle link (Fig. 3 *u—w*), but I also found, quite unexpectedly, some cases of ring-and-rod trivalents (Fig. 3 *x*) and one clear ring of three (Fig. 3 *y*).

Chains of four chromosomes were also met with (Fig. 3 *z*, *aa*),

which were evidently built up of the two heterobivalents, although the size differences were not always clear.

This pairing situation goes to show that the plant was a segmental interchange hybrid. It may be assumed that two chromosome pairs have been changed in a manner suggested in the scheme of Fig. 3 *bb—ee*. In this scheme, however, the size differences are exaggerated. The variation in size observed within the heterobivalents may be explained thus: in one case *bb* has paired with *cc* and *dd* with *ee* (see the scheme), while in another case the two pairs are *bb—dd* and *cc—ee*. The larger heterotrivalent consists of *bb cc ee* and the smaller of *bb dd ee*. The observed ring-and-rod configuration can be explained in this latter case by *dd* and *ee* forming two chiasmata, one on each side of the centromere, while *bb* forms a chiasma within the white section of *dd* (see the scheme). Such a ring as is shown in Fig. 3 *y* should not occur, however. Both chains and rings of four may originate, although the latter of these configurations was not found. Since one chiasma per chromosome pair is the rule in sugar beets, associations of four should be rare. In spite of this interchange, which must result in a deficient genic quantity of some of the gametes, the pollen fertility of the plant was fairly good (82 %).

3. THE TRISOMICS.

Twenty trisomic plants were studied and nine of them could be analysed in some detail. When trisomics are concerned, it is more than usually important to make a parallel study of the morphology and cytology of the plants, especially as a preliminary of further studies on the phenotypic effect of each chromosome of the beet genome. Therefore I shall here give a short description of the appearance of each of the nine trisomic plants which were studied cytologically.

18107—30. — Erect, leaves broad, oblong, rounded, thick, brittle, surface fine-buckled, colour dull, light-green, edge smooth, somewhat rolled upwards, petioles short, vigour very good. This plant probably belongs to the »lettuce-type». Shooting of flower stalks took place rather late. Pollen fertility 55 %.

Trivalents and univalents from this plant are pictured in Fig. 4 *a—f*. The extra chromosome is one of the medium-sized chromosomes. There often occurred an interstitial chiasma in the trivalent. In the diploids, too, one such chiasma per cell is sometimes found, although I cannot judge for the present whether one particular bivalent has the tendency

of incomplete chiasma terminalization. The univalent was seen in 38 cells of 72.

18107—34. — Semiprostrate, leaves short, broad, of medium thickness, surface with transversal furrows, normal-green, somewhat glossy, edge coarsely indented, petioles white, as long as or longer than the

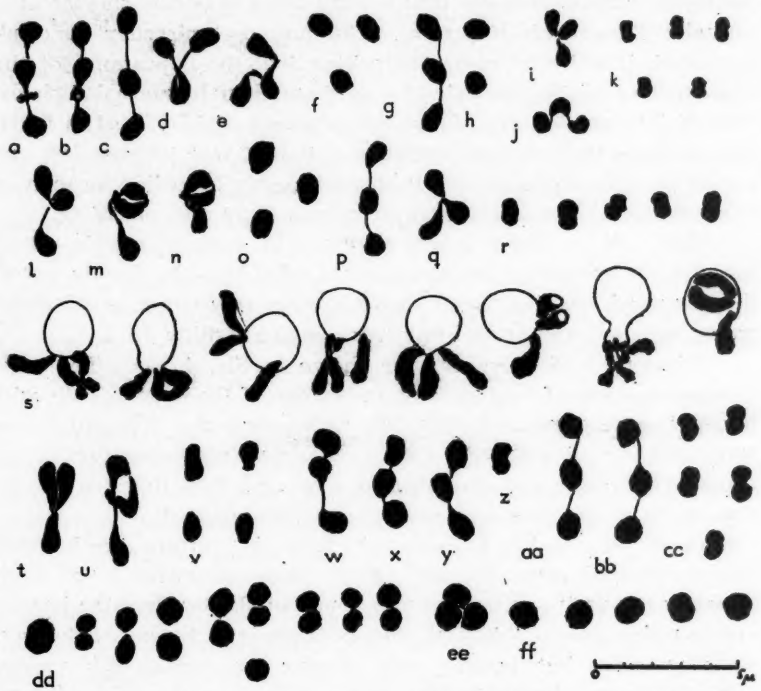

Fig. 4. Meiosis of trisomic plants, *a—f*: 18107—30, *g—h*: 18107—34, *i—k*: 18107—41, *l—o*: 18107—44, *p—r*: 18112—28, *s—v*: 18112—61 (the nucleolar trisomic), *w—z*: 18112—83, *aa—cc*: 18112—89, *dd—ff*: 18112—123. — × 2400.

lamina, vigour very good. Agrees with the »bullate-type» but lacks its dark colour. Normal shooting, 85 % good pollen.

One trivalent and two univalents from this plant are shown in Fig. 4 *g, h*. The extra chromosome was of medium size and probably among the smaller chromosomes. The univalent was seen very frequently, it was counted in 43 out of 59 cells.

18107—41. — Semi-erect, leaves triangular-oblong, of medium thickness, surface smooth, somewhat furrowed along the nerves, colour

dark, somewhat glossy, edge smooth, petioles long, white, vigour very good. Does not fit into any of the described trisomic types. Shooting normal, 62 % good pollen.

Trivalents and univalents are shown in Fig. 4 *i*—*k*. The extra chromosome was the absolutely smallest one studied, which is partly due to the chromosome size of this plant being decidedly smaller than normally. Since such properties as chromosome contraction are gene-controlled, it is by no means surprising that the appearance of the chromosomes of the trisomics varies more than in normal diploids. Even if this smaller size of the chromosomes of 18107—41 is taken into account, the extra chromosome certainly was the smallest one among the trisomics studied. It showed clearly a median location of its centromere. The univalent was counted in 29 cells out of 49.

18107—44. — Erect, leaves oblong, thin, surface smooth, colour light, glossy, somewhat anthocyanin-red, edge smooth, slightly rolled, shooting good, also the flower shoots had the very characteristic light-green, narrow leaves, rolled upwards. Pollen fertility 78 %.

Trivalents and univalents are shown in Fig. 4 *l*—*o*. The extra chromosome was of medium size, rather one of the larger. Cells with trivalents were commoner than cells with univalents. The latter type was counted in 6 among 21 cases. The trivalents were often of the ring-and-rod type, and it happened now and then that one of the chiasmata of the ring was incompletely terminalized (Fig. 4 *m*—*n*).

18112—28. — Erect, leaves oblong-ovoid, surface fine-buckled, colour yellowish-green (mosaic), glossy, edge somewhat erose, some tendency to upward rolling, petioles long but shorter than the lamina, vigour rather poor. A typical »mosaic-trisomic». Flower stalks were shooting early, but became very slender and weak with narrow chlorotic leaves. Pollen fertility 57 %.

Its chromosomes are shown in Fig. 4 *p*—*r*. The extra chromosome was of medium size or rather large. It was present as a univalent in 43 out of 54 cells. Disturbances were often observed also in the other two chromosomes of the trivalent. Thus two of them forming a bivalent could be located outside the plate, or all three chromosomes could be present in the form of univalents.

18112—61. — Semi-erect, leaves oblong, thin, surface smooth somewhat fine-buckled, glossy, colour bluishly green (strong anthocyanin colour), edge erose, rolled upwards, petioles red or reddishly yellow, long, but shorter than the laminae, somewhat similar in habit to the horseradish, vigour medium; the nucleolar trisomic. Early

shooting, the viability in the flowering stage very poor. 40 % good pollen.

Fig. 4 *s—v* shows chromosomes of this plant at diakinesis and metaphase I. At diakinesis it may be seen in favourable slides, almost in every cell, that three chromosomes are associated with the nucleolus. At metaphase, univalents were comparatively rare; they were counted in 24 out of 90 cells. Also at metaphase it may be seen that the extra chromosome is submedially inserted.

18112—83. — Erect, leaves with very long rather narrow lamina, surface smooth or fine-buckled, in some places irregularly creased, colour dull, yellowishly green, edge smooth, often rolled, petioles long, but shorter than the laminae, appearance abnormal, »frost bitten», vigour medium. Late shooting, normal appearance in the flowering stage. 90 % good pollen.

Chromosomes from metaphase I are shown in Fig. 4 *w—z*. The extra chromosome was of medium size, rather one of the larger. It sometimes appeared monstrously swollen. The univalent occurred in 25 out of 71 cells.

18112—89. — Semi-prostrate, leaves broad, triangular, thick, brittle, surface fine-shrivelled, colour dark-bluish-green, glossy, edge coarsely crispy, irregularly folded upwards, petioles very long, in the largest leaves up to 1,7 times the length of the lamina. Appearance normal, vigour very good. Agrees fairly well with the »bullate» type. Shooting late, flower stalks with leaves folded upwards, 97 % good pollen.

Its meiotic chromosomes are shown in Fig. 4 *aa—cc*. The extra chromosome of medium size, rather on the small side. Its centromere is clearly medially located.

18112—123. — Semi-prostrate, leaves long, irregularly shaped, thin, surface smooth or fine-buckled, colour dull, light-green (somewhat chlorotic), edge erose, petioles long, often turned round 180°, so that the lower surface of the leaves get turned upwards. Habit abnormal, also the main nerves of the laminae are turned and bent. Vigour rather poor. Shooting early, leaves of the flower stalks not abnormal, but very narrow and with long petioles. Pollen fertility 86 %.

Fig. 4 *dd—ff* shows metaphase I. The extra chromosome is large, maybe the largest chromosome of the idiogram. The univalent was counted in 46 out of 70 cells. As is seen in the pictures, the chromosomes of this plant had a deviating shape. They were strongly con-

tracted so that both the univalents and the chromosomes of the bivalents and trivalents were spherical and not as is usual pear-shaped. Possibly genes in the extra chromosome bring about this excessive chromosome contraction.

In this plant later stages of the first division were also observed. It was seen that the univalent at late anaphase moves towards the equator and is divided there. A chromatin bridge was noticed a couple of times. At the first telophase 88 cells with univalent were analysed. Among them the univalent was distributed at random in 75 cases and divided at the equator in 13 cases. The second division was usually free from vagabonding chromosomes.

It is quite clear that the few instances of trisomics which have so far been studied cytologically do not allow of any generalizing of the results. The differences noticed in size between the different extra chromosomes are so small that it is difficult to be sure that they represent real differences. With this reservation, however, I cannot refrain from pointing out that a certain correlation is discernible between the size of the extra chromosome and the vigour of the trisomic: the vigour of the plant shows a decrease with an increasing extra chromosome. The plant with the smallest extra chromosome (18107—41) had a viability score of 7, the plants with a smaller medium size of their extra chromosomes (18107—30, —34, 18112—61, —89) had on an average a viability of 7, the plants with larger medium-sized extras (18107—44, 18112—28, —83) had a viability of 6, while, finally, the plant with the largest extra chromosome (18112—123) had a viability of 5.

The frequency of univalents as compared with trivalents does not show any such agreement. It might have been expected that the number of cells with trivalents would increase with an increasing size of the extra chromosome. That is not the case. Grouped in the same way according to increasing size of the extra chromosomes, the percentage of cells with univalents is as follows: $59{,}2$, $52{,}9$, $47{,}8$, $63{,}9$. Evidently other factors than mere chromosome size are operative here.

4. 20-CHROMOSOME PLANTS.

Two such plants were planted in the greenhouse. Both were above the average in vigour among the 20-chromosome plants in the field. Both shot in the greenhouse, but only one gave usable fixations (18107—45). Its chromosomes are shown in Fig. 5 *a*, *b*. It was a

double trisomic which often formed two trivalents per cell. The frequency of different configurations was counted in the following cells:

Configuration	2_{III}	$1_{III} + 1_{I}$	2_{I}	Total
Number of cases.....	28	39	7	74

The two extra chromosomes were somewhat different in size, the smaller being of medium size, the larger being one of the largest chromosomes of the idiogram.

5. MORE THAN 36 CHROMOSOMES.

One 42-chromosome plant (18112—148) and one 45-chromosome plant (18114—10) were fixed. They had both very good vigour also

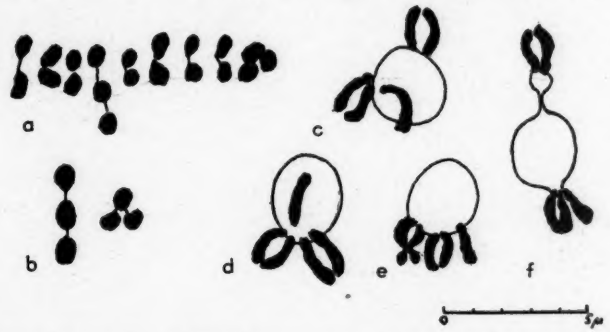

Fig. 5. Metaphase I of a double trisomic (*a*, *b*) and the nucleolar chromosomes at diakinesis of the 42-chromosome plant (*c*—*f*). — × 2400.

in the flowering stage. Only the 42-chromosome plant gave good fixations, metaphase I was missing in the slides, however. So I shall only give a few pictures of the nucleolar chromosomes at diakinesis (Fig. 5 *e*—*f*). Five nucleolar chromosomes were present. They were often attached to the nucleolus in two groups, one group with three and one with two chromosomes.

VI. GENERAL CONSIDERATIONS.

1. DIPLOID—TRIPLOID CROSSES.

A comparison has been made between the results obtained in the reciprocal crosses between diploid and triploid sugar beet and some

earlier known cases of such crosses. Table 4 is a compilation from different studies of the same species (e. g. *Datura stramonium*, *Populus tremula*), or of different species and hybrids of the same genus (*Oenothera biennis*, *Lamarckiana*, *biennis* × *Lamarckiana*, *muricata* × *Lamarckiana*, *decipiens*, *rubricalyx*). The composition in percentage of the progenies has been divided into five groups: the diploid and the triploid numbers, these classes comprising only one chromosome number each, and the chromosome numbers situated between these two classes. These are divided into three equal-sized groups, the absolute size of which may consequently vary depending on the value of the basic number (x). They are always $= \frac{x-1}{3}$, and the limits of the groups are: 2x, $2x + \frac{x-1}{3}$, $2x + \frac{2(x-1)}{3}$, and $3x - 1$. If the limit between two classes falls within one chromosome number, the value of this number has been divided proportionally between the two classes. The mean of each progeny has been expressed in percentage of x in order to make it comparable as between materials with different x-values ($2x = 0$, $3x = 100$, $4x = 200$).

From Table 4 it is seen that two types of distributions occur in the 11 cases recorded: *1.* The most common type (cases 1—6, 8—9) is characterized by the presence of a marked difference between the two reciprocal types of crosses, and *2* (cases 7, 10, 11) characterized by no or little difference between the reciprocals.

Group 1. — In the direction 2x × 3x the progenies are characterized by the 2x class being the most frequently represented class. Intermediate class 1 (= »i1») is often represented too, especially because of the presence of some trisomics, although always in lower frequency than the pure diploids; only in case 4 (*Allium*) is i1 totally absent. I2, lying in the middle between 2x and 3x, is lacking in all instances. I3 is lacking in *Zea*, *Oenothera* and the Solanaceae, while 6—21 % fall within it in *Fragaria*, *Allium*, and *Beta*. This is mostly due to plants with the chromosome number 3x — 1, only in *Allium* there also occur a few plants with the number 3x — 2. In 3x, single individuals of *Allium*, *Beta* and *Zea* occur, while the genera lack triploids. The mean of this cross is always lower than the mean of the reciprocal cross. In most cases the mean is situated between 2x and 2x + 10 % of x, only in *Allium* and *Beta* the mean reaches 2x + 23 % and 12 % respectively, owing to the plants occurring at and below 3x.

The reciprocal crosses 3x × 2x of Group 1 are markedly differ-

TABLE 4. *Diploid—triploid crosses.*

Case	Genus	x	Mother plant	The composition of the progeny					Number of plants	Mean in % of x	Author
				2x	Intermediate class			3x			
					1	2	3				
1	*Fragaria*	7	2x	81,8	9,1	0,0	9,1	0,0	11	8,6	YARNELL, 1931
			3x	37,5	54,1	4,2	4,2	0,0	24	14,3	
2	*Oenothera*	7	2x	87,9	12,1	0,0	0,0	0,0	66[1]	1,4	VAN OVEREEM, 1921; DE VRIES and BOEDIJN, 1924; BOEDIJN, 1925; DULFER, 1926; CAPINPIN, 1933
			3x	14,3	56,6	19,5	8,3	1,3	456	28,6	
3	*Petunia*	7	2x	87,0	13,0	0,0	0,0	0,0	92	1,4	DERMEN, 1931; MATSUDA, 1935; LEVAN, 1937
			3x	19,4	63,4	10,8	5,4	1,1	93	22,0	
	expected			0,8	21,9	54,7	21,9	0,8	—	—	
4	*Allium*	8	2x	74,6	0,0	0,0	21,0	4,2	71	22,5	LEVAN, 1936 b
			3x	27,6	36,7	13,8	15,0	6,9	29	31,3	
	expected			0,4	21,4	56,5	21,4	0,4	—	—	
5	*Beta*	9	2x	77,1	12,6	0,0	6,3	4,1	48	12,3	LEVAN, the present paper
			3x	9,8	61,4	18,3	9,3	1,2	82	28,9	
	expected			0,2	19,7	60,2	19,7	0,2	—	—	
6	*Zea*	10	2x	73,0	24,3	0,0	0,0	2,7	37	6,0	MCCLINTOCK, 1929
			3x	0,0	50,0	40,0	10,0	0,0	10	34,0	
	expected			0,1	17,1	65,6	17,1	0,1	—	—	
7	*Tulipa*	12	2x	20,0	72,0	1,3	6,7	0,0	25	15,0	UPCOTT and PHILP, 1939
			3x	0,0	38,7	49,3	12,0	0,0	50	41,7	
8	*Solanum*	12	2x	100,0	0,0	0,0	0,0	0,0	2	0,0	LESLEY, 1928
			3x	16,4	83,6	0,0	0,0	0,0	61	9,2	
9	*Datura*	12	2x	85,7	14,3	0,0	0,0	0,0	7	0,8	BELLING and BLAKESLEE, 1922; BLAKESLEE, 1927; SATINA, BLAKESLEE and AVERY 1937, 1938
			3x	27,8	72,2	0,0	0,0	0,0	982	7,5	
	expected			0,0	15,3	69,3	15,3	0,0	—	—	
10	*Pyrus*	17	2x	0,0	46,3	33,3	20,0	0,0	25	41,2	DARLINGTON and MOFFET, 1930; NEBEL, 1933; DERMEN, 1936; JOHANSSON, 1937; WANSCHER, 1939
			3x	0,0	37,5	50,6	10,5	1,4	215	41,3	
	expected			0,0	10,3	79,4	10,3	0,0	—	—	
11	*Populus*	19	2x	15,1	20,0	37,5	25,9	1,5	614	44,7	BERGSTRÖM, 1940; JOHNSSON, 1940
			3x	12,0	20,1	49,4	18,7	0,0	75	43,2	
	expected			0,0	8,4	83,3	8,4	0,0	—	—	

[1] These 66 plants were selected for cytological investigation by VAN OVEREEM from among 423 plants as being more or less deviating in type from normal diploids. The remaining 357 plants were probably all diploids.

ent. Pure diploids are rare, in *Zea* they are totally missing, in the other materials their frequency varies between 10 % and 40 %. I1 is the commonest class. The trisomic number is most frequent, although it does not dominate so much over the other numbers, as the diploids did in 2x × 3x. In *Solanum* and *Datura*, however, the trisomic number constitutes 50 % and 60 % of the progenies. The whole i1 comprises 37—83 %, mean frequency = 60 %. I2, totally missing in 2x × 3x, is usually present here. It is lacking in *Solanum* and *Datura* but is represented in the other cases by 4—40 %. I3 occurs somewhat more rarely. It is lacking in *Solanum* and *Datura*. Its frequency in the rest of the material is 4—15 %. Pure triploids occur with few individuals in *Oenothera*, *Petunia*, *Allium*, and *Beta*.

Thus, the difference between the reciprocal crosses in Group 1 is mainly due to the fact that the intermediate classes, which according to pure expectation should be the commonest classes, are lacking if 3x is used as pollen parent, while they are formed, though in a much less degree than expected, if 3x is used as mother plant. As is well known, this condition can be ascribed to the differences in gametic selection, depending on whether the extra chromosomes are carried by the pollen or by the egg-cells. This will be discussed under paragraph 3 of the present chapter.

Group 2. — This includes the three genera *Tulipa*, *Populus* and *Pyrus*. It is characterized by the difference between the reciprocals being less prominent. In *Pyrus* and *Populus* the two reciprocals have about the same mean, while in *Tulipa* 2x × 3x has a decidedly lower mean than 3x × 2x. *Tulipa*, in fact, constitutes a transition to Group 1 and could with equal right have been combined with this group, an arrangement which is adopted by JOHNSSON (1940). *Tulipa* is placed by me in Group 2 mainly because Group 1 is characterized by the 2x class in 2x × 3x being the largest class throughout, and all numbers between 2x + 2 and 3x — 2 being lacking, two conditions which are not fulfilled by *Tulipa*. The distributions of Group 2 evidently show a better agreement with the binomial distribution, and so the gametic selection seems to be less strict than in Group 1. On no less than seven occasions the euploid numbers are missing, which they would be expectedly almost everywhere. As JOHNSSON points out, the differences between Groups 1 and 2 are not to be regarded as qualitative but only as quantitative, depending on how far the gametic and zygotic selection has acted. It is suggestive in this connection that Group 1 includes types with lower chromosome numbers (x = 7—12), in which evidently

extra chromosomes may be expected to cause the greatest disturbance of the genic balance, while Group 2 comprises higher chromosome numbers (x = 12—19), which for different reasons may be considered as crypto-polyploids.

The difference between Groups 1 and 2 is demonstrated in the two graphs of Fig. 6. A mean frequency of the different materials is represented by the drawn line (2x × 3x) and by the dotted line (3x × 2x), *a* shows the conditions of Group 1 and *b* of Group 2. In

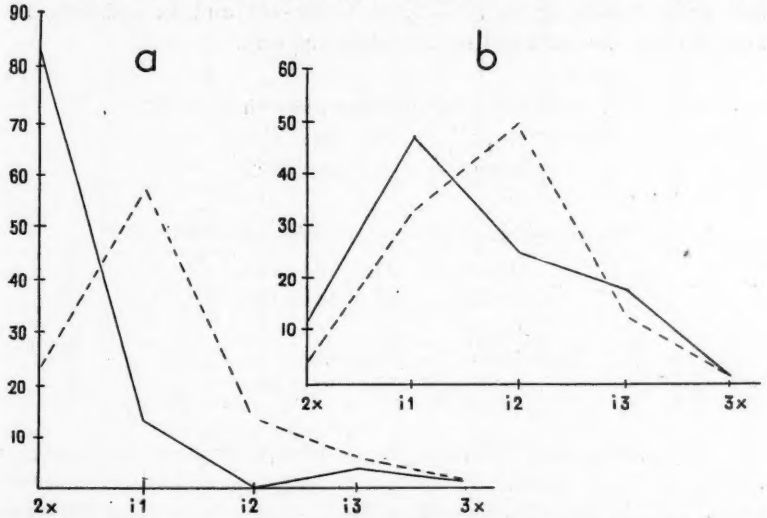

Fig. 6. Scheme of the two types of 2x—3x-crosses. *a*: Group 1, the reciprocals are different, *b*: Group 2, the reciprocals are similar. Drawn line = 2x × 3x, dotted line = 3x × 2x.

both cases the curve of 3x × 2x is situated to the right of the reciprocal curve. In Group 1 the course of the two curves is quite dissimilar, while in Group 2 the two curves agree in their main features.

2. TRIPLOID—TRIPLOID CROSSES.

We have next to consider what happens when triploid pollen is allowed to fertilize triploid plants. The main part of the material discussed in this paper consists of such progenies. In Table 5 this material is compared with 3x × 3x progenies of seven other genera. In order to make a comparison possible in spite of differences in the basic number, a similar grouping of the material has been made as in

the preceding paragraph. The chromosome numbers of the 3x × 3x progenies are situated between 2x and 4x, and in addition there often occur some higher numbers, resulting from unreduced gametes.

Group 1. Low basic numbers. — A study of those materials of Table 5 where the basic numbers are low (cases 1—7) reveals the presence of two types of progenies: *1.* those having the bulk of the material gathered in the vicinity of the 2x-class, and *2.* those progenies in which most of the plants approach 4x. If each progeny is divided into three groups, 2x to 3x — 1, 3x to 4x — 1 and 4x upwards, the material may be arranged in the following way:

1. The first class contains more than 50 %.

Crepis:	78,3;	20,9;	1,0;
Beta:	56,3;	41,2;	2,4.

2. The second or third class contains more than 50 %.

Oenothera:	31,1;	55,1;	13,8;
Petunia:	22,0;	60,0;	18,0;
Avena:	16,1;	74,2;	9,7;
Allium:	6,6;	86,0;	7,4;
Triticum:	0,0;	9,7;	90,3.

A detailed scrutiny of the different curves shows certain common features in their course. If *Triticum* is excepted, which has no values below 4x — 2, and *Petunia*, where the 3x-region is lacking, the other five curves agree in the following respects: one maximum at 2x, one minimum between 2x and 3x, one maximum at 3x, a new minimum between 3x and 4x, and one maximum somewhat below 4x. The last maximum is not present in *Crepis*.

The start of the curves is as follows: either the curve falls directly from 2x towards the first minimum, when the fall may be very steep (*Crepis*) or more shallow (*Avena*, *Petunia*), or the curve rises from 2x to 2x + 1 or 2x + 2 and then falls again to the first minimum (*Oenothera*, *Allium*, *Beta*). In *Beta* the highest point of the entire curve is located at 2x + 2, and therefore the grade is rather steep, in *Allium*, on the other hand, the increase to 2x + 1 is slight (the chromosome classes 2x to 2x + 4: 7, 8, 5, 4, 0). The first minimum is often so complete that one or more classes are not formed at all. Thus the following classes are absent: in *Oenothera* 2x + 3, 5 and 6, in *Avena*

TABLE 5. *Triploid—triploid crosses.*

Case	Genus	x	The composition of the progeny										Number of plants	Mean in % of x	Author
			2x	Intermediate class			3x	Intermediate class			4x	>4x			
				1	2	3		4	5	6					
1	*Crepis*	3, 4	58,4	11,9	4,0	4,0	11,9	3,0	3,0	3,0	1,0	0,0	101	35,2	HOLLINGSHEAD, 1930
	expected	4	0,4	3,1	10,9	21,9	27,3	21,9	10,9	3,1	0,4	—	—	—	
2	*Triticum*	7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	9,7	41,5	48,8	41	245,0	THOMPSON, 1931
3	*Avena*	7	8,1	4,0	0,8	3,2	0,8	0,0	9,7	63,7	9,7	0,0	124	151,8	NISHIYAMA, 1934
4	*Oenothera*	7	3,4	24,2	3,5	0,0	3,4	17,2	31,0	3,5	10,4	3,4	29	114,0	VAN OVEREEM, 1921
5	*Petunia*	7	8,0	10,0	4,0	0,0	0,0	0,0	0,0	60,0	10,0	8,0	50	165,7	DERMEN, 1931; MATSUDA, 1935; LEVAN, 1937
	expected		0,0	0,6	8,3	30,6	21,0	30,6	8,3	0,6	0,0	—	—	—	
6	*Allium*	8	1,1	2,3	0,6	2,6	3,4	4,9	25,0	52,7	6,1	1,3	619	160,0	LEVAN, 1936 a
	expected		0,0	0,5	7,8	31,9	19,6	31,9	7,8	0,5	0,0	—	—	—	
7	*Beta*	9	5,2	34,3	6,9	9,9	7,3	13,0	13,6	7,3	0,5	1,9	368	80,2	LEVAN, the present paper
	expected		0,0	0,3	6,9	33,6	18,6	33,6	6,9	0,3	0,0	—	—	—	
8	*Populus*	19	5,5	6,8	18,2	27,3	18,2	16,6	5,2	1,6	0,7	0,0	308	94,4	JOHNSSON, 1942
	expected		0,0	0,0	1,7	41,9	12,9	41,9	1,7	0,0	0,0	—	—	—	

2x + 2 and 3, in *Allium* 2x + 4. In *Crepis* and *Beta* all classes occur, the least represented being 2x + 3 and 4 in *Crepis*, and 2x + 4 in *Beta*.

The maximum at 3x is usually rather slight. It is most pronounced in *Crepis*, where 12 % lie in the 3x class, while the adjoining classes have 3—4 %. *Avena* has its maximum at 3x + 1 and it is a very trifling one, and the situation in *Oenothera* and *Allium* is similar. In *Beta* the second maximum is low (7 %) and the grades up to it are very gradual, 18 % lying between 3x — 1 and 3x + 1. The second minimum between 3x and 4x is, as a rule, less pronounced than the first one. In *Oenothera* and *Avena*, however, one or two classes are entirely missing. The least represented class in *Oenothera* and *Allium* is 3x + 1, in *Beta* 3x + 2, in *Avena* 3x + 1 and 2. As already mentioned, the *Crepis* curve falls directly from 3x to 4x. All the others have a third mode below or at 4x, and in all genera except *Beta* this mode constitutes the top point of the whole curve. The mode lies rather low in *Oenothera* (4x — 4 and 5), in *Avena* and *Allium* it is situated at 4x — 2, in *Petunia* at 4x — 1, and in *Triticum*, finally, at 4x. In *Beta* the third maximum is rather vague, still vaguer than the second maximum. In any case its centre of gravity is not located higher than at 4x — 3, probably all classes from 3x + 2 to 4x — 2 belonging to the third maximum.

Single plants are formed above 4x, in *Triticum* even the bulk of the progeny falls here. These chromosome numbers may have been formed by non-disjunction gametes containing more than 2x chromosomes; this being the case with those chromosome numbers which lie close above 4x. The higher chromosome numbers have been formed by the fusion of one doubled and one normal gamete (5x) or two doubled gametes (6x). Close above 4x the following values occur: *Triticum* has 8 plants with 4x + 1, 3 with 4x + 2, *Petunia* 4 with 4x + 1, *Allium* 4 with 4x + 1 and 1 with 4x + 2, *Beta* 2 with 4x + 1 and 1 with 4x + 2. In the region around 5x (the fourth maximum) single plants occur in *Triticum* (2 with 5x — 1, 5 with 5x), in *Allium* (1 with 5x — 2, 1 with 5x — 1), and in *Beta* (1 with 5x — 3, 2 with 5x — 1, 1 with 5x). At 6x *Triticum* has 2 plants (6x) and *Allium* 1 plant (6x — 3).

Group 2. High basic chromosome number. — The only 3x × 3x progeny studied in Group 2 is the *Populus* progeny published in another paper of the present issue of Hereditas (JOHNSSON, 1942). As seen from this paper, p. 307 and Fig. 1 (p. 308), and from the last rows of my Table 5, the triploid progeny of *Populus* shows quite interesting properties. While the chromosome class 2x constitutes a clear maximum

and 4x also shows a weak indication of a maximum, the 3x-class is the absolutely predominating top point of the curve. Although the curve is similar to the binomial distribution, there are certain important deviations. Thus, the 3x-class as well as the wing classes (2x to 2x + 12 and 4x to 4x — 12) shows a surplus of variates, while considerable deficits are found at both sides of 3x (3x — 4 to 3x — 1 and 3x + 1 to 3x + 5). The left half of the curve has a much greater surplus than the right part, from which fact JOHNSSON draws the conclusion that the viability of the aspen is better below than above 3x.

This triploid progeny constitutes a clearly defined type, deviating from all triploid progenies of Group 1. As pointed out by JOHNSSON, this is caused by the high basic number of *Populus*, and its probable crypto-polyploidy. Therefore this 3x × 3x cross should rather be compared with 6x × 6x crosses.

3. THE GAMETIC AND ZYGOTIC SELECTION IN TRIPLOID PROGENIES.

As we have seen from the foregoing, the distributions of chromosome numbers found in triploid progenies usually differ very much from the binomial distribution that would have been expected if purely statistical factors were determinative. Instead, an elimination of certain chromosome classes and a favouring of other classes is brought about in various stages of the development of the gametes and the zygotes. This selection already starts at the meiosis of the triploid. As x bivalents are always formed, all gametes will receive at least x chromosomes, but the remaining x chromosomes, the »odd» chromosomes, are distributed at random at the first meiotic division. The chromosome number of the gametes should therefore form a binomial curve from x to 2x with its maximum at 1,5x. Deviations from this curve are due to different causes; one important factor is the elimination of extra chromosomes during meiosis, which will cause a displacing of the curve to the left, the mean becoming less than 1,5x. These conditions have been directly studied in the first pollen mitosis of suitable material. UPCOTT and PHILP (1939) point out that besides purely genotypic factors, which favour gametes with certain chromosome combinations, also cell-mechanical factors play an important part in the chromosome elimination. The relative size of chromosomes and cells is of importance. The elimination of extra chromosomes is greatest in organisms with small chromosomes and large cells, where the way the chromosomes have to go from the equator to the poles is the longest. For

the same reason the elimination should be more pronounced in the embryo-sac mother cells than in the pollen mother cells of the same plant.

The gametic selection is for several reasons less strict on the female side than in the pollen. It may be supposed that, if the chromosome equipment of the embryo-sac has at least so much viability that it can complete mitoses, there is a chance for a mature egg-cell to be formed. The egg-cells are present in a relative paucity, with the result that even cells with a rather weak chromosome combination may be fertilized. The conditions of the pollen are quite different. The pollen must stand severe strains, disengage from the nourishing tissue of the pollen sac, germinate on the stigma, and grow down through the style under strong competition. It should be noted that according to the binomial distribution the lower the chromosome number of the pollen is, the greater percentage of euploid pollen is formed, and the greater is the chance that euploid pollen tubes will grow past the aneuploid tubes and fertilize all the egg-cells present. With the aid of BUCHHOLZ's technique it has been directly demonstrated in *Datura* that the euploid pollen tubes grow faster than the aneuploid tubes. In this material it has also been shown that pollen tubes with certain kinds of extra chromosomes grow faster than tubes with other combinations of extras. As could be expected, it is consequently the genotype of the pollen which determines its competition value, not its chromosome number, even if in most materials the numerical variation only is approachable for study.

Immediately after the fertilization the zygotic selection starts. It is determined by the genotypic constitution of the zygote as well as by the environment of the young embryo. At the earlier stages this environment results mainly from the co-operation of three kinds of tissues: the mother plant, the embryo and the endosperm. In triploid progenies these conditions are of special interest, as the chromosome relations of the three tissues vary. Besides two basic genomes the endosperm will contain twice the extra chromosomes of the egg-cell and once the extras of the pollen. MÜNTZING (1933) has especially pointed out the significance of the numerical chromosome balance between mother plant, embryo and endosperm. In a normal diploid this relation is 2 : 2 : 3. In a cross $2x \times 3x$ the first factor is 2, while the chromosome number of the embryo varies from 2 to 3, simultaneously as the chromosome number of the endosperm varies from 3 to 4. Thus, the range of variation is 2 : 2 : 3 to 2 : 3 : 4. In *Beta* with its basic

number 9 the following five combinations were realized in this type of cross: 18 : 18 : 27, 18 : 19 : 28, 18 : 20 : 29, 18 : 26 : 35, 18 : 27 : 36, and in *Allium* (x = 8) the following four: 16 : 16 : 24, 16 : 22 : 30, 16 : 23 : 31 and 16 : 24 : 32. In the cross 3x × 2x these relations vary from 3 : 2 : 3 to 3 : 3 : 5. In *Beta* all of them were realized, in *Allium* all except 24 : 20 : 32 (i. e. 3 : 2,5 : 4).

In the crosses 3x × 3x the conditions are somewhat more variable. The variation goes from 3 : 2 : 3 to 3 : 4 : 6, but while these two extremes only have one kind of endosperm each, the intermediate classes have two or more types of endosperm, depending on which type of gametic combinations has fused. Therefore the embryonic class 3x, which may originate from x + 1 kinds of combinations, has x + 1 kinds of endosperm with chromosome numbers varying from 4x to 5x.

The chromosome number relation *mother plant : embryo : endosperm* seems to be of less importance in these crosses than the chromosome constitution of the embryo. Otherwise the classes around 3x in the 3x × 3x-progeny would be especially favoured with their rich selection of accessible types of endosperm. Instead, most of the beet descendants fall in the range $3 : (2\frac{1}{9} - 2\frac{2}{9}) : (3\frac{1}{9} - 3\frac{4}{9})$ and most of the *Allium* descendants in the range 3 : (3,5—4) : (5—6). The only genus where the 3x-class is in great excess is *Populus*. In *Allium* the chromosome number 20 fails, the relations being 2 : 2,5 : 3,5, 3 : 2,5 : 4 or 3 : 2,5 : (3,5—4).

The selection of zygotes continues during the seed development. Triploids and diploids fertilized with triploid pollen always show a decreased seed production as compared with selfed or intercrossed diploids. In 2x × 3x crosses and reciprocally the triploids as female parents usually give more seed than the diploids, and the seeds of the triploids have a better germination power (see Fig. 11 in UPCOTT and PHILP, l. c.). The conditions were different in the 2x × 3x-sugar beet cross, the diploid plant yielding almost double the quantity of seeds, while the seeds of the triploid plant showed about three times better germination. The two beet plants used in this cross were of about the same size, but as the number of flowers were not counted, no conclusions can be drawn from the deviating result.

The germination of the seeds constitutes the next viability test. Only a very small part of the triploid seeds will grow, although their appearance is normal (the germination percentage of the triploid beet seeds was 4 % on an average). At this point the chromosome numbers

of the seedlings may be determined and a picture of the selection thus far occurring may be obtained. The gametic selection is inferred from the reciprocal 2x × 3x-crosses, where the direction 3x × 2x gives an idea of the frequency with which the ♀-gametes have functioned. The picture is disturbed, it is true, by zygotic selection having taken place between the fertilization and the seed germination, but it represents the most reliable picture available. The left part of the 3x × 3x zygotic curve (from 2x to 3x) is directly comparable with the zygotic curve of 3x × 2x. Differences between these distributions must be due to the occurrence of gametes with extra chromosomes in the pollen of the triploid. How the triploid pollen functions within diploid tissue, is shown in the cross 2x × 3x.

The distributions of chromosome numbers in the 3x × 3x progenies show characteristic maxima and minima, the former situated at the euploid numbers, the latter between them. If the curves are considered in their entire length, it is found that the different maxima and minima are differently developed. One factor which determines the total course of the curves is the location of the viability optimum, which varies in different materials. The euploid number situated closest to the viability optimum tends to become the top point of the curve. The next paragraph will deal with these conditions in *Beta*, *Allium* and *Populus*, which react differently in this respect. It is characteristic of most materials that the first maximum and minimum are the most pronounced. Among the lower chromosome numbers between 2x and 3x the balance of the genotype is easier upset than in the higher chromosome numbers. These conditions are especially evident in such a plant as *Allium nutans*, in which I have been able to study the relative viability of representatives of a considerably wider range of chromosome numbers than in *Allium Schoenoprasum*, plants with chromosome numbers varying from 16 to 108 being accessible in *Allium nutans*. While the maxima 1, 2 and 3 are quite distinct from each other, it is found that Nos. 4 and 5 are rather indistinct and that the maxima 6, 7 and 8 fuse completely together.

4. THE FREQUENCY OF ZYGOTES WITH DIFFERENT CHROMOSOME NUMBERS IN TRIPLOID PROGENIES OF BETA, ALLIUM AND POPULUS.

An attempt will now be made to analyse the frequency of zygotes in the 3x × 3x progenies of *Beta* and as far as possible also in *Allium* and *Populus*. By using the ♀-gametic frequency inferred from the cross 3x × 2x I shall try to obtain some idea of the frequency with

which the ♂-gametes must have functioned to produce a zygotic series such as is met with in the 3x × 3x progeny. *Beta* and *Populus* are the first instances concerning which tolerably ample data from these three types of crosses are available. Especially the region between 2x and 3x of the 3x × 3x crosses is well represented and makes an analysis possible.

At first a test was made to ascertain whether the same gametic frequency could have functioned in the ♂- as in the ♀-gametes of *Beta* (for the ♀-gametic frequency see Table 1, row 1). As is seen from Table 6, third row (expectation 1), this assumption is evidently untenable. The observed values are quite too low in the middle of the curve and too high in the wings. This indicates that as compared with the euploid classes the intermediate classes of the pollen have had much less play than is implied in this assumption.

Next, a zygotic series is constructed by using the same ♀-gametes against the ♂-gametic frequency encountered in the cross 2x × 3x (Table 1, row 2). The result is given in Table 6, expectation 2. Now the entire left part of the curve of the observed values is too low (the classes 18—25), while all classes above 25 are too highly represented. This shows that the percentage of x pollen functioning and giving viable zygotes in the cross 2x × 3x (78 %) is considerably higher than what must be the case in 3x × 3x. The entire course of the curve, however, indicates that this type of pollen frequency, viz. numerous euploid x and 2x pollen and few pollen grains of the intermediate classes and some 2x — 1 and possibly also 2x — 2, is what has actually functioned in principle.

A purely mathematical attempt was made by the method of the smallest square to solve the problem as to which combination of ♂-gametes gives together with the postulated ♀-gametes the zygotic distribution obtained in the 3x × 3x cross. Although mathematically correct the solution turned out to be absurd, some gametic classes being represented by negative values. This shows that the actual premises of the equations were erroneous. In order nevertheless to get somewhat nearer a solution of the problem the following empirical calculations were employed: The zygotic class 18 in 3x × 3x represented by 19 individuals must have been formed by 9-chromosome pollen fusing with 9-chromosome egg-cells. The class 19, represented by 48 individuals, has been formed by egg-cells with 9 chromosomes and 10 chromosomes respectively. These two types of egg-cells are supposed to be present in the same proportions as in the 3x × 2x cross,

TABLE 6. *Test of different male gamete frequencies in Beta, Allium and Populus.*

	2 n	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
Beta	found	19	48	65	20	6	9	11	9	20	27	21	11	24	15	20	21	11	2	2	
	binomial...	0,0	0,0	0,2	1,1	4,2	11,8	25,6	43,8	60,3	67,0	60,3	43,8	25,6	11,8	4,2	1,1	0,2	0,0	0.0	
	expected 1	3,4	16,3	38,3	56,9	58,8	46,7	33,9	27,7	24,6	20,2	14,3	8,7	4,7	2,7	1,8	1,1	0,5	0,2	0,1	
	expected 2	27,3	66,8	82,1	58,9	26,9	18,8	16,1	12,2	10,8	11,4	10,3	8,1	3,9	2,0	1,8	1,6	1,1	0,6	0,2	
	expected 3	8,7	25,7	38,1	35,8	25,2	20,4	21,3	24,4	28,7	33,5	33,1	25,7	15,1	8,2	6,5	5,0	3,2	1,7	0,6	

	2 n	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32			
Allium	found	7	8	5	4	0	2	6	9	21	9	14	20	60	122	185	101	38			
	binomial...	0,0	0,2	1,1	5,2	17,0	40,7	74,7	106,7	120,0	106,7	74,7	40,7	17,0	5,2	1,1	0,2	0,0			
	expected 1	46,5	104,6	70,5	36,5	26,9	49,5	66,7	42,1	62,5	32,0	20,4	11,5	12,3	14,5	5,8	5,8	2,9			
	expected 2	126,0	141,5	16,0	31,5	0,0	63,0	25,0	68,2	69,1	13,6	7,4	6,5	14,2	9,1	9,8	8,3	1,8			
	expected 3	3,7	6,1	5,0	6,5	10,0	20,7	46,8	82,6	112,1	79,8	36,7	47,9	49,6	42,0	24,8	23,7	13,0			

	2 n	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
Populus	found	17	3	2	4	5	6	1	5	10	11	11	8	11	4	11	13	12	23	21	56
	binomial...	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,2	0,5	1,4	3,0	6,1	10,8	17,3	24,0	32,3	37,6	39,6
	expected 1	4,4	2,0	5,2	1,1	5,3	2,9	4,6	5,5	7,8	13,0	13,7	12,8	15,4	12,6	14,9	11,9	17,0	16,1	16,7	16,4
	expected 2	5,6	2,7	4,4	2,4	4,5	4,2	4,1	5,7	7,4	11,2	13,5	11,4	15,2	13,7	13,9	13,6	14,4	14,9	13,5	14,8
	expected 3	6,8	2,6	6,8	1,2	6,6	3,5	5,3	6,6	9,2	15,3	15,5	13,7	16,7	12,0	15,1	11,9	17,1	15,5	15,6	15,2

	2 n	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	
Populus	found	13	15	3	5	6	9	1	8	3	0	3	1	0	3	0	1	0	1	2	
	binomial...	37,6	32,3	24,9	17,3	10,8	6,1	3,0	1,4	0,5	0,2	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	
	expected 1	15,4	15,6	13,8	11,9	11,7	10,4	9,1	6,0	5,1	3,5	2,2	1,5	1,3	0,9	0,2	0,0	0,0	0,0	0,0	
	expected 2	14,4	14,4	14,4	13,0	12,1	10,8	9,5	7,9	6,1	5,0	3,3	2,5	1,5	1,0	0,6	0,4	0,1	0,0	0,0	
	expected 3	13,9	13,9	11,9	10,4	10,0	8,8	7,7	5,1	4,4	3,1	1,9	1,5	1,1	0,8	0,3	0,2	0,1	0,0	0,0	

viz. 8 : 19 (Table 1, row 1). Consequently in $\frac{8}{27} \times 48$ 10-chromosome pollen has functioned, in $\frac{19}{27} \times 48$ 9-chromosome pollen, and so on. By summing up all pollen frequencies thus obtained the following series of ♂-gametes resulted:

n =	9	10	11	12	13	14	15	16	17	18
%	25,9	13,0	5,9	3,9	4,2	5,3	7,4	9,3	10,7	14,4

As is seen, these values constitute an even and plausible curve. Its general tendency resembles the curve used in the preceding test, although the intermediate classes are more frequently represented and the difference in proportion between x and 2x is decidedly levelled.

This ♂-frequency tested against the ordinary ♀-gametes results in the zygotic distribution of expectation 3 in Table 6. Broadly speaking, the agreement is here much better than in the two earlier cases, expectations 1 and 2. Still, it must be said that the agreement is very unsatisfactory. The observed values are considerably higher in the wings of the curve and lower in the middle. This new series, too, underestimates the importance of the euploid numbers in relation to the intermediate classes. None the less, there is no doubt that the general principles of this pollen frequency are correct. And it is certainly of importance to realize that while the curve of the ♀-gametes is convex, the ♂-gametes form a concave curve in building up the triploid progenies. Without these very palpable calculations it is perhaps not quite evident that the ♀- and ♂-gametes actually function in frequencies which are images of each other.

It was noted several times during these considerations that the intermediate classes took up too large a space in the ♂-gametic distribution. We will now test what the result will be if the intermediate classes of the pollen are completely eliminated: can the triploid curve be explained solely on the assumption that the postulated ♀-gametic frequency acts together with x and 2x pollen? In order to test this the zygotic curve is divided into two regions: 2x—3x and 3x—4x. The first question will be: is there any difference between the ♀-gametic curve 9—16 and the zygotic curve 18—25? The classes 17, 18 and 26, 27 respectively have been excluded, while in these classes 2x pollen also interferes. The following two series are compared:

Zygotes 18—25: 19, 48, 65, 20, 6, 9, 11, 9
Gametes 9—16: 8, 19, 22, 14, 5, 4, 4, 3

A test of homogeneity, in which the last four classes are combined two and two, gives a χ^2 of 3,8946 with 5 degrees of freedom, which shows that the curves with a high degree of probability are identical. Thus, it is evident that this part of the zygotic curve may very well be explained by the assumption that exclusively x pollen has functioned.

The next question is: can the agreement between the two series be improved by assuming the functioning of a few x + 1 and x + 2 pollen grains together with the x pollen? We select the proportions found in the 2x × 3x zygotes, viz. a relation between 9 : 10 : 11-chromosome pollen of 37 : 3 : 3 (Table 1). From the frequency of the ♀-gametes and these numbers the expected proportions of zygotes 18—25 are calculated. The following comparison results:

Zygotes 18—25:	19,	48,	65,	20,	6,	9,	11,	9,
Calculated proportions:	6,88,	19,90,	20,81,	14,91,	6,82,	4,77,	4,07,	3,14

It is seen that the agreement has become somewhat impaired, χ^2 being 7,3092. Although this gives a probability of 0,20, it is evident that no improvement has been brought about. Thus, it is probable that the pollen classes x + 1 and x + 2 take less part in the zygote formation in 3x × 3x than in 2x × 3x. Or biologically expressed: the x pollen grains are in a more favourable position as compared with the neighbouring aneuploid classes when growing in 3x tissue than in 2x tissue.

The next problem to be dealt with is the question of the relative proportion of x and 2x pollen in the progenies 2x × 3x and 3x × 3x. Is the relation the same or has it been altered? We have already in the foregoing got an indication that the relation is changed, for the pollen frequency of 2x × 3x tested against the ♀-gamete frequency of 3x × 2x gave an excess of the entire left half of the curve (Table 6, expectation 2). It was then concluded that in reality more ♂-gametes with numbers close to 2x function in 3x × 3x than in 2x × 3x. It remains to test whether this assumption holds good statistically. The relation between x and 2x pollen is 43 : 5 in the cross 2x × 3x and 220 : 141 in the cross 3x × 3x (on calculating this latter number the value of class 27 has been divided into halves, as no absolutely correct division can be made, and small changes certainly can have no influence on the result). A χ^2 of 15,1311 with 1 degree of freedom is obtained, which means a very significant difference. Thus, the part

taken by the x pollen in the zygotic production is essentially lower in 3x × 3x than in 2x × 3x. Evidently the pollen grains with higher chromosome numbers are more successful in forming zygotes in the triploid than in the diploid.

The right part of the zygotic curve in 3x × 3x will now be studied: can the zygote numbers above 3x be explained by the functioning of 2x pollen against the known ♀-gametic frequency? In the classes 26 and 27 those variates are excluded which may be assumed to have originated from x pollen. Their number is calculated from the number of zygotes in the classes 18—25 of the 3x × 3x curve as related to the same number of the 3x × 2x curve, i. e. 187 : 79 = 2,3671. Consequently, 4,73 and 2,37 are subtracted from the values of the classes 26 and 27 respectively. Then the following two series are to be compared:

Zygotes 27—36:	25,	21,	11,	24,	15,	20,	21,	11,	2,	2
Gametes 9—18:	8,	19,	22,	14,	5,	4,	4,	3,	2,	1
χ^2:	1,6869	2,7231	14,5071	0,0535	0,8876	3,3390	3,9809		0,3869	

$\Sigma\chi^2$ is 27,7850, and thus it may be said that there is no agreement between the two series. Especially the χ^2 of the class 29 is high, owing to a great deficit in the zygotic value. Consequently, it may be concluded that the zygotes have not been formed from the known ♀-gametic curve through the functioning of exclusively 2x pollen.

The question whether a better agreement can be secured by using both 2x and 2x — 1 pollen in the proportions 3 : 2 (Table 1, row 2) was also tested. This test gave the following series:

Zygotes 26—36:	15,	25,	21,	11,	24,	15
Calculated proportions:	4,8,	14,6,	20,8,	17,7,	8,6,	4,4
χ^2:	0,6838,	0,2710,	5,3179,	10,6747,	0,6416,	0,9327
Zygotes 26—36:	20,	21,	11,	2,	2	
Calculated proportions:	4,0,	3,4,	2,4,	1,4,	0,4	
χ^2:	2,8958,	4,4153,	1,0692			

As seen from this, χ^2 (26,9020) has not been improved by this operation.

It can consequently be concluded that the intermediate classes of the pollen play a greater part in the upper half of the triploid curve than among the low-chromosomic zygotes. This condition may probably be explained in the light of the fact that the viability curve of the zygotes takes quite a different course in the region 3x—4x from that taken in the region 2x—3x, where it is directly reproducible in the

3x × 2x crosses. This means that the elimination of the intermediate classes is less pronounced in the upper half of the zygotic curve. It should also be remembered that 13- and 14-chromosome pollen grains in triploid beets are formed 250 times more often than 9-chromosome pollen, a relation which is augmented still more by the chromosome elimination at meiosis, so the change in the viability conditions does not need to be very considerable in order to give an entirely new importance to the intermediate classes.

Summarizing the results of the above operations, the following may be stated. The ♀- and the ♂-gametes function in the 3x × 3x crosses with quite different frequencies. While the frequency of ♀-gametes still retains certain features of the binomial distribution, the ♂-gamete frequency forms a concave curve. In the 3x × 3x progenies the zygotes below 3x may be explained on the assumption that only x pollen has functioned. The pollen classes x + 1 and x + 2, which were shown to function in the 2x × 3x cross, participate to a less degree in 3x × 3x. The functioning proportion x : 2x pollen is different in 3x × 3x from that in 2x × 3x, 2x pollen grains being more prevalent in the cross 3x × 3x. The zygotes situated between 3x and 4x in the progeny 3x × 3x cannot be explained on the basis of the ♀-gametic frequency in 3x × 2x, which is due to the zygotic viability obeying other laws in this region than in the region 2x—3x.

Attempts were also made on the basis of the gametic frequencies found in the 2x × 3x crosses to analyse the course of the 3x × 3x curve in *Allium*. The original material for these frequencies is found in LEVAN, 1936 a, Table 13 and in LEVAN, 1936 b. As already pointed out in connection with Tables 4 and 5 of the present paper, the *Allium* curves differ very conspicuously from the *Beta* curves. Especially striking is the difference between the two 3x × 3x progenies, where in *Beta* the centre of gravity is situated between 2x and 3x, while in *Allium* it is situated in the neighbourhood of 4x. Thus in *Beta* only 36,5 % of the progeny lies above 3x, while in *Allium* the same value is no less than 90 %. Typical in *Allium* is the total absence of 20-chromosome plants. This somatic number has never been realized in any *Allium* species with x = 8. On the whole it may be said that *Allium* is characterized by a stricter selection of zygotes than *Beta*. The viability of the zygotes in *Allium* increases very much towards 4x, and this is why the high chromosome numbers are formed in such an excess.

These considerations suffice to show that it must be still more

difficult in *Allium* than in *Beta* to reconstruct the zygotic frequencies of the 3x × 3x cross from the gametic frequencies such as they are met with in the 2x × 3x crosses. Still, I made the same calculations in *Allium* as are recorded above in *Beta*, and the results are collected in the middle portion of Table 6. In expectation 1 the found ♀-gametic frequencies of 3x × 2x have been used also for the ♂-gametes. No agreement with the found values can be seen. In expectation 2 the ♀-gametic frequencies of 3x × 2x were combined with the ♂-gametic values of 2x × 3x. Also here there is no agreement. Finally, a similar calculation as in *Beta* was made, the ♂-gametic frequencies being extracted from the found zygotic values of the 3x × 3x curve. The following series of ♂-gametes resulted:

n =	8	9	10	11	12	13	14	15	16
%	2,4	1,3	1,5	1,8	3,1	7,8	19,6	28,3	34,2

This series evidently constitutes an image of the ♀-gamete curve, as was the case also in *Beta*. In the ♀-gametes the highest values are found to the left in the curve, which drops towards the right. As the absence of 12-chromosome ♀-gametes in this curve is due to the non-formation of the zygotic class 20, while without doubt 12-chromosome gametes may function in other combinations, an adjustment of the ♀-gametic curve was made, the class 12 receiving a value calculated from the classes 10, 11, 13 and 14. Reduced to percentages the following ♀-gamete values were obtained:

n =	8	9	10	11	12	13	14	15	16
%	24,9	28,0	3,2	6,2	9,6	12,5	3,2	6,2	6,2

The result in crossing the two gametic series thus obtained is shown in Table 6, expectation 3. Although the agreement with the found values is somewhat better in this series than in expectation 1 and 2, it must be said that it is very bad, especially in the highest classes. No tested gametic frequency has been able to bring about the gathering of zygotes found in the classes 28—32.

Owing to the scarcity of those variates which fall between 2x and 3x in the 3x × 3x *Allium* curve, it is impossible to test statistically whether this distribution may be produced by exclusively x pollen.

The indisputable similarity between this distribution and the zygotic distribution in 3x × 2x, however, makes such an assumption rather plausible. In the region 3x—4x it is certain, though, that another gametic distribution has functioned with its main bulk decidedly displaced to the right. 81,7 % of the entire progeny must have been formed exclusively from 14-, 15- and 16-chromosome pollen.

The differences in behaviour observed between *Beta* and *Allium* may be ascribed in a high degree to differences in the action of the zygotic selection. While in *Beta* the differences in viability of different chromosome classes certainly are very pronounced, yet the entire series of chromosome numbers is represented rather richly. In *Allium*, on the other hand, the viability of the classes between 2x and 3x is very poor, so relatively few such zygotes are formed.

A third case, in which both reciprocal 2x × 3x and 3x × 3x progenies exist, is *Populus*. This case represents a type entirely deviating from *Beta* and *Allium*. Its high basic chromosome number makes the effect of each single chromosome on the viability less important both in the gametes and in the zygotes. Consequently, *Populus* differs from the genera with a lower basic number in certain respects. As already mentioned, the reciprocal 2x × 3x crosses give almost identical results, both progenies being more or less similar to the binomial distribution. The result of the 3x × 3x crosses also is broadly speaking binomial. The difference between the 2x × 3x crosses and the 3x × 3x can be characterized thus, that the former crosses lack a very prominent maximum, which is present in the latter crosses. JOHNSSON (1942) shows that this difference is due to the maximum of 2x × 3x lying halfway between two euploid numbers, while the maximum of 3x × 3x coincides with a euploid number.

The testing of what functioning gametic frequencies may result in the observed zygotic frequency is for various reasons of less interest in this case. The result of the 2x × 3x differs very little from 3x × 2x. Further it may be seen that the 3x × 3x distribution has originated from the intercrossing of two somatic series of a rather excessive binomial type. The same calculations as in *Beta* and *Allium* were made, however, the result being given in the lower part of Table 6. As in the earlier cases »expected 1» means the zygotic frequency $(3x \times 2x)^2$, »expected 2» is calculated from the zygotic frequency 3x × 2x crossed with 2x × 3x, and »expected 3», finally, is the 3x × 2x series crossed with an empirical ♂-gamete frequency calculated in the same way as in *Beta* and *Allium*. It is found that in neither case is the agreement

very satisfactory. All the three gametic frequencies employed lack sufficient over-representation in the middle classes to be able to bring about the excessive maximum at 3x of the zygotic curve.

In conclusion it should be pointed out that *Beta*, *Allium* and *Populus* represent three different types of triploid progenies. In *Beta* the bulk of the material gathers down between 2x and 3x, and all chromosome classes theoretically expected are rather well represented. The 3x × 3x-distribution may be reconstructed from the reciprocal 2x × 3x-crosses without very much difficulty. *Allium*, on the other hand, has most of its 3x × 3x-progeny approaching the tetraploid chromosome number, while several lower numbers are entirely or almost entirely missing. The correlation between the 2x × 3x- and the 3x × 3x-crosses is very difficult to trace. In *Populus* all three progeny curves, 2x × 3x, 3x × 2x and 3x × 3x, are rather similar, all of them approximating the binomial distribution. The differences between them may clearly be ascribed to differences in zygotic selection.

These striking differences in behaviour of the three analysed triploid materials make the danger of generalizing in this kind of work especially obvious.

5. THE VIABILITY OPTIMUM OF THE SUGAR BEET.

From a practical point of view the most important among those questions which have been taken up for investigation in the present work is undoubtedly the question of what region of chromosome numbers furnishes the optimal conditions for the development of the sugar beet. This question has been illumined from different sides in the preceding pages; it has not, however, been definitively answered. It was shown that certain indications may be gathered from the study of solely the frequencies of viable chromosome numbers. It must be assumed that the facility with which the zygotes within a certain region of chromosome numbers are realized in the triploid progenies constitutes an index of the relative viability of the plants within this region. The prime condition of viability is that the zygote in question can be formed at all. Thus, it is found that most of the triploid progenies analysed show a tendency to approaching the tetraploid chromosome number. Such is the situation, for instance, in *Triticum*, *Avena*, *Petunia* and *Allium*, and in these materials, therefore, the primary viability optimum may be assumed to lie closer to 4x than to 2x. In *Beta*, on the other hand, the chromosome numbers were more evenly distributed, the centre of gravity, however, lying below 3x.

The *a priori* situation of the viability is therefore somewhat different in *Beta* from that in the other materials.

The cultivation experiments of plants with different chromosome numbers in *Beta* should be able to locate the definitive viability optimum, which is determined by the response of the different chromosome numbers to the environment. Unfortunately, my experiments were seriously impaired by certain conditions, already pointed out several times. Above all, the vegetation period of the plants was altogether too short, which resulted in the beets being far from mature at the harvest. As polyploids usually need a longer vegetative period than corresponding diploids, it is evident that because of the curtailed growth season the

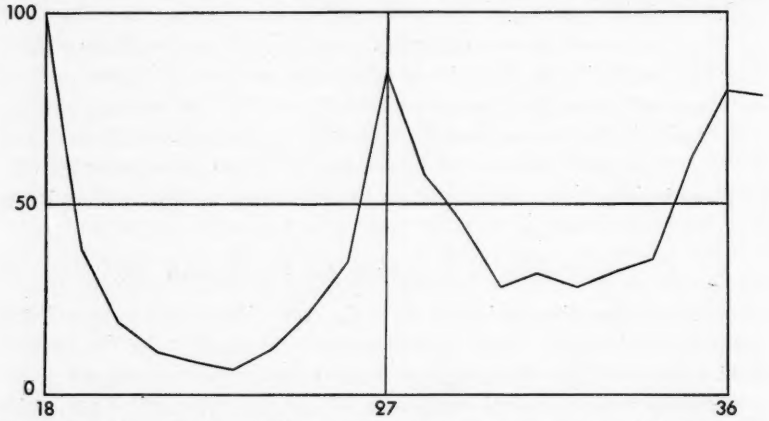

Fig. 7. The curve of root weights for different chromosome numbers in sugar beets.

diploid beets were unduly favoured as compared with triploids and tetraploids. We know now from other experiments that triploids and tetraploids are not always so inferior in comparison with the diploids as is indicated by the present results.

With these reservations a graph is given in Fig. 7 showing the means of the root weights of different chromosome numbers expressed in percentages of the diploid value (Table 2, col. 7). It is seen that this curve is very even and regular. As pointed out earlier, the root weights constitute a collected measure of the physiological production capacity of the sugar beet, and this curve is therefore less influenced by casual disturbances than other viability curves. It is probably very reliable as far as it goes, i. e. it demonstrates the productivity of the different chromosome numbers after a growth period of $3\,^1/_2$ months.

The curve would undoubtedly have assumed quite another appearance had the vegetation period been of normal length. The curve shows the two deep minima, No. 1 deeper than No. 2, which are characteristic of viability curves. It also gives some indications concerning the relative viability of the three euploid numbers. These constitute the three modes of the curve.

The 3x and 4x modes of some of the studied qualities are collected in the following survey, all 2x-values being equal to 100:

	3x	4x
1. General viability (field estimation)	79,7	67,1
2. Weight of the tops	99,3	92,0
3. » » » roots	83,7	79,7
4. Length of the petioles	81,4	83,3
5. » » » leaves	99,4	115,3
6. Breadth » » »	105,4	115,0
7. Number » » »	84,3	67,2
Mean 1—7	90,5	88,5
» 1—3	87,6	69,1

Only in the case of the leaf dimensions there is an increase from 2x to 4x, in the other qualities an obvious falling tendency is present. This means that the chromosome optimum of the sugar beet in these experiments is situated at 2x.

PETO and BOYES (1940) arrive at a different result in the sugar beet variety »Great Western». 56 triploid plants showed after a vegetation period of about 9 months an increase of the mean weight by 12,2 % as compared with the diploid control plants. While the sugar content was about the same in diploids and triploids, the triploids yielded 14,9 % more sugar per root. The proportions of the leaves were also changed, the triploids having 15,6 % greater length and 16,8 % greater breadth. According to these experiments the triploid number should be closer to the optimum in *Beta* than the diploid number. Unfortunately, the small number of plants makes it impossible to draw any general conclusions from these experiments, which is also pointed out by the writers.

SCHLÖSSER (1940) has studied triploid and tetraploid sugar beets of the variety »Klein Wanzleben E». He finds that the development of the diploids is more rapid than of the polyploids: »Die Polyploiden sind gewissermassen physiologisch jünger als die gleichalten diploiden

Formen» (l. c., p. 38). The quantity of each leaf is larger, however, in the polyploids. When the diploids had developed their seventh leaf, the five first leaves showed the following weights of green matter: 6224 mgm. (2x), 7555 mgm. (3x) and 9981 mgm. (4x). The corresponding dry-matter values were 482, 550 and 618 mgm. The tetraploids thus produce in their five first leaves 49 % more green matter and 28 % more dry matter than the diploids. Although SCHLÖSSER does not find that the polyploid sugar beets show a greater definitive productivity than the diploids, as his experiments were discontinued after two months, he points out, supported by results among others in the tomato, that in spite of their slower development the polyploids may reach an »entwicklungsphysiologischer Umschlagspunkt» at which the increase in quantity of the polyploids passes the diploids. According to my results this point has not been reached in the sugar beets after a period of $3\,^1/_2$ months. PETO and BOYES, however, mention that at the transplanting of the beets into the field (viz. after $4\,^1/_2$ months) the triploids of their experiments were slightly larger than the diploids, »and the difference in size became more pronounced as the season advanced» (l. c., p. 274).

Thus, the question of the situation of the optimal chromosome number region in the sugar beet hangs together with a great many other questions, the genotype of the material, the conditions of culture, the length of the growth period, etc. Even if the genic combinations which are now prevalent in the ordinary commercial varieties of sugar beet have their optimum at 2x, it is certainly within the limits of possibility that a selection among the 4x material will produce genic combinations which are able to compete with the present diploid materials or even surpass them.

SUMMARY.

The present paper is a morphological study of plants with different chromosome numbers in sugar beets. The material (Tables 1 and 3) consists of reciprocal 3x × 2x-progenies and 3x × 3x-progenies and comprises all somatic numbers between 2x and 4x (Chapter I).

The following morphological characters were studied: the general vigour of the plants, the weight of the tops and the roots, different characters of the leaves, the refraction of the sap, different cell properties, size of stomata, size of plastids (Table 2). It was found that all the viability characters formed a typical curve (Fig. 7): maxima at

the euploid numbers and minima between them, the minimum between 2x and 3x being more pronounced than that between 3x and 4x. This is very plainly demonstrated in Fig. 1 *a* and *b*, where typical leaves are represented from plants with different chromosome numbers (Chapter II).

The cell size shows the ordinary increase with increasing chromosome number. The same is the case with the nucleolus. The size of the plastids shows no clear correlation to the chromosome number (Chapter III).

The occurring trisomic plants can be assigned to a few morphological groups, each group presumably corresponding to a certain extra chromosome. Five such groups are described (Chapter IV).

Meiosis is studied in one diploid structural hybrid, in the trisomics, triploids and in 2 ± pentaploids (Chapter V, Figs. 2—5).

In a chapter devoted to general considerations (Chapter VI) a survey is given of different 2x × 3x-crosses (Table 4, Fig. 6) and 3x × 3x-crosses (Table 5). The presence of different types of triploid progenies is discussed from various angles, *Beta*, *Allium* and *Populus* being dealt with in some detail (Table 6). The probable location of the viability optimum of the sugar beet in a certain chromosome number region is discussed.

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SOME EXPERIMENTS ON C-MITOTIC REACTIONS WITHIN CHLOROPHYCEAE AND PHAEOPHYCEAE

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ONE of the most important questions that has arisen during the extensive work with colchicine reactions, started by the discovery of the specific effect of colchicine on the mitotic mechanism, is the question of the different sensitivity of organisms to the one or the other of the substances producing c-mitosis. While all Phanerogams, with the exception of *Colchicum*, seem to be equally sensitive to colchicine and, including *Colchicum*, to acenaphthene, there are very distinct differences in the reaction of higher plants to other substances, as, for instance, α-mono-chlor-naphthaline. Generally whole families behave in the same manner, all members being either immune or sensitive (LEVAN, unpublished).

Among the Cryptogams very few investigations have as yet been made on the influence colchicine and other c-mitotic substances have on the chromosome mechanism and the cell division mechanism. This is of course partly due to the great technical difficulties with which chromosome studies are associated in most lower organisms. A cross section through the literature shows that nothing is known about the colchicine reactions of Cyanophyceae, Diatomeae, Characeae, Phaeophyceae, Rhodophyceae, Myxomycetes, Phycomycetes, and Lichenes. In Bacteria OBATON (1939) observed that the divisions in *Photobacterium phosphoreum* occurred more rapidly under the influence of colchicine. GAVAUDAN and KOBOZIEFF (1938), and VANDENDRIES and GAVAUDAN (1939, 1941), studying certain lower organisms, found that colchicine, even in strong solutions (1 %), has no effect on the cell divisions, whereas acenaphthene checks the growth in some cases and brings about an abnormal development. These writers seem to ascribe this effect to a toxic action, »un arrêt banal de la croissance», rather than to the induction of c-mitoses. This condition is found in *Euglena* (Flagellatae); *Chlamydomonas*, *Gonium*, *Polytoma* (Chlorophyceae, Volvocales); *Closterium*, *Micrasterias* (Conjugatae, Desmidiales). Col-

chicine is without effect in fungi (Miss SATINA in BLAKESLEE, 1939). GAVAUDAN and collaborators have studied *Coprinus* and *Psilocybe* (Basidiomycetes) and found no effect from 1 % colchicine. The same is true of common yeast (BEAMS, ZELL and SULKIN, 1940), while RICHARDS (1938) even found a certain stimulation of the budding process of *Saccharomyces* to be effected by colchicine. BAUCH (1941 a and b) reports a positive reaction of yeast to acenaphthene, camphor and α-naphthene-amine, quite new forms of yeast originating, which remain constant on further culture. Since in some cases they constitute giant races, BAUCH interprets them as tetraploid and octoploid races. Among the Bryophyta two Hepaticae are known to react positively to colchicine, viz. *Marchantia* (Miss SATINA in BLAKESLEE, l. c.) and *Pallavicinia* (WOLCOTT, 1941). Also in some Pteridophyta the same response to colchicine has been found as in higher plants (ROSENDAHL, 1941).

MATERIAL AND METHODS.

The present paper is the first of a series intended to treat the c-mitotic reactions of certain plant groups concerning which little is known in this respect. For the present some results are given of experiments with two *Ulva* species (Chlorophyceae) and two representatives of Phaeophyceae, *Ectocarpus* and *Spermatochnus*. The culture experiments were performed at Kristineberg Zoological Station, Bohuslän. Zoospores of the algae or, in the case of *Ulva lactuca*, young zygotes were brought to attach to slides. The treatments were started 12 or 24 hours after the attachment to the slides, before any cell divisions had taken place. Thus, the starting-point in each case was one single cell. This makes it easy to study differences in growth and mitotic rhythm between the controls and the treated materials.

The experiments with colchicine were performed in the following way: four slides with the young cells were placed in one glass jar with sea water to which was added certain nutrient substances (0,01 % $NaNO_3$, 0,002 % Na_2HPO_4 and 2 drops iron citrate solution per 150 cc culture fluid). To this nutrient medium colchicine was added so that three different concentrations resulted, viz. 1, 0,1 and 0,01 %.

At the experiments with acenaphthene a somewhat different arrangement was necessitated because of the very slight solubility of acenaphthene in water. The slides with the young cells were therefore placed in a moist chamber, a few drops of the nutrient solution covering the spores. In the chamber a small dish with acenaphthene crystals was placed, the vapours of acenaphthene thus being allowed to act on

the young cultures. The thin layer of nutrient solution was renewed every two or three days. This arrangement turned out to be very satisfactory for the culture of the young algae.

The slides were fixed at different intervals after the beginning of the treatments, the first fixations being made after one day, the last after 38 days. NAVASHIN was used as fixing fluid. The stainings were made in gentian violet, acid fuchsine and iron haematoxyline, the best cytological results being achieved in this last-mentioned staining.

ULVA LINZA.

This species is propagated exclusively by zoospores with four cilia. Twelve days after attachment to the slides the plants of the untreated control cultures had grown out into threads consisting of 10—15 cells, not counting the rhizoid cells. The appearance of one normal plant is seen in Fig. 1 *a*. The plants cultivated for 12 days in acenaphthene atmosphere showed a strikingly different appearance (Fig. 1 *b*—*g*). Most of them were still unicellular, and no plants with more than two cells were present. In the latter case one cell division might have taken place before the influence of the acenaphthene had asserted itself. Although the cells of the treated plants were somewhat larger than the cells of the controls, the difference in size was not very pronounced. The chromosomes of *Ulva* are very difficult to detect, but a close study revealed a great many mitoses in the control material (Fig. 1 *h*, *i*). The chromosomes are small and spherical (Fig. 1 *i*). In side views the spindle was clearly seen, and in polar view we tried to determine the chromosome number. It turned out to be impossible, however, to analyse whole equatorial plates; so we had to be content with an estimation of the number at 24—25 chromosomes, possibly the figure is somewhat higher. This number is of the same size order as the diploid number found in *Ulva lactuca* (FÖYN, 1934), and so *Ulva linza* is supposedly diploid.

In the material treated for 12 days no spindles were found, and the chromosomes could be seen to be scattered out irregularly all over the cells (Fig. 1 *k*—*m*). They were clearly arranged in pairs, although the components of some pairs were located far from each other. These chromosome pairs were present in a number corresponding to the number of chromosomes estimated in the untreated material. The appearance of the pairs was very similar to the ordinary c-pairs found in higher plants after colchicine treatment. It is of interest that a treatment of nine days, although resulting broadly speaking in the same

picture as a treatment of twelve days, still showed a few traces of the spindle, as, for instance, remnants of unipolar spindles. Acenaphthene

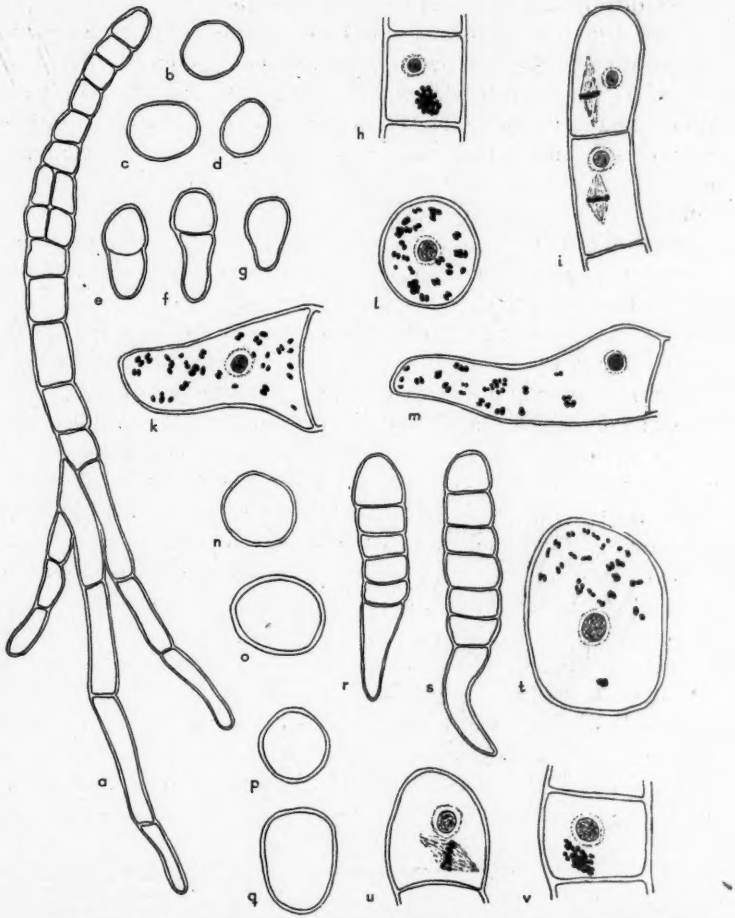

Fig. 1. *a—m*: *Ulva linza*, 12 days, *a*: the general appearance of an untreated plant, *b—g*: plants treated with acenaphthene, *h—i*: metaphase of untreated cells (note the pyrenoid), *k—m*: c-mitosis in cells treated with acenaphthene; *n—v*: *Ulva lactuca*, 10 days, *n—q*: general appearance of plants treated with acenaphthene, *r—s*: untreated plants, *t*: c-mitosis in a treated cell, *u—v*: untreated cells with normal metaphase: — *a—g*, *n—s* × 600; *h—m*, *t—v* × 1200.

thus seems to act rather slowly, the spindles first being formed and then again broken down.

Thus, the situation seems to be the following: Under the influence of acenaphthene the prophase goes on normally and the nuclear membrane dissolves. The spindle apparatus has been destroyed by the acenaphthene; so the chromosomes do not congregate into an equatorial plate but spread out all over the cell. The chromosome-halves finally fall apart when the centromeres divide. So far, the process is quite typical and agrees with the conditions in higher plants. In *Ulva*, however, no continuation of this first c-mitosis could be found: while the cells of the control plants had undergone mitosis four or five times resulting in a 10—15-cellular plant, the treated material showed signs of only one c-mitosis. Evidently acenaphthene brings about a considerable retardation of the mitotic rhythm in *Ulva*. It would be of great importance for the interpretation of the c-mitosis in *Ulva* to continue the treatment longer in order to furnish a possibility of ascertaining whether the first c-mitosis in *Ulva* is followed, as in higher plants, by new c-mitoses. It will also be necessary to try to keep the plants alive for a time after the treatment in order to investigate whether the induced abnormalities of the spindle are reversible, which is so characteristic of the c-mitosis of higher plants. Until these tests are performed it is not possible to say whether an identical mechanism is working in *Ulva* as in the higher plants.

The experiments with colchicine yielded results which were somewhat different from the above results. Colchicine turned out to be less effective in checking the mitoses. Even in the 1 % solution some cells divided once. After a couple of days all cells died in this strong solution, evidently through poisoning. In a 0,1 % solution certain disturbances were seen, but numerous mitoses occurred, although the mitotic rhythm was decidedly slower than in the controls. In a 0,01 % solution, on the other hand, the cells divided rapidly and the plants grown for two weeks in this solution could hardly be distinguished from the controls of the same age.

ULVA LACTUCA.

Our experiments with this species agree with the above results and can therefore be described somewhat more summarily. The starting-point in this case was unicellular zygotes resulting from recently conjugated gametes. The treatments started 12—24 hours after the attachment of the zygotes to the slides. The growth of *Ulva lactuca* is somewhat slower than that of *Ulva linza*. After ten days the control plants had undergone 3—4 mitoses, and hence, besides the still unicellular

rhizoids, there were present 5—6 cells (Fig. 1 *r—s*). All plants treated with acenaphthene for ten days were unicellular (Fig. 1 *n—q*), no bicellular plants being found as in *Ulva linza*. This difference was probably due to the slower division rate of *Ulva lactuca*, no mitosis having had time to take place before the action of the acenaphthene was complete.

Mitoses were studied in the untreated plants (Fig. 1 *n—v*). An exact determination of the chromosome number was also impossible in this species, about 25 chromosomes being counted. This number agrees with the number given by FÖYN (1934, p. 160) for diploid *Ulva lactuca*, viz. at least 26 (as a rule only about 20 chromosomes were visible). In haploid plants the number 13 was counted by FÖYN.

The treated cells of *Ulva lactuca* (Fig. 1 *t*) showed the same characteristics as have already been described for *Ulva linza*. About 25 c-pairs were scattered out over the entire cell. The difference in cell size is apparent on comparing *r—s* with *n—q* in Fig. 1. The response to the different colchicine concentrations was the same in this as in the former case. 1 % solution killed the plants after a few days, 0,1 % solution delayed the development but did not prevent the mitosis, 0,01 % solution had no visible effect.

ECTOCARPUS SILICULOSUS AND SPERMATOCHNUS PARADOXUS.

In both cases zoospores were brought to germination on the slides. The appearance of untreated plants of *Ectocarpus* grown for ten days is seen in Fig. 2 *a* and of *Spermatochnus* in Fig. 2 *g*. The treatment with acenaphthene gave about the same result as the 0,1 % colchicine (Fig. 2 *c—f*, *l—p*). Very few mitoses had taken place, the plants being uni-, bi- or, seldom, tri-cellular. Especially in *Spermatochnus* each cell was decidedly larger in the treated plants than in the controls. Unfortunately we were not able to study the chromosomes; so we cannot decide whether c-mitoses are started by these treatments. 1 % colchicine solution killed the plants almost immediately. The cultures in 0,01 % colchicine differed very slightly from the controls (Fig. 2 *b*, *h—k*). In *Spermatochnus* a mixture of perfectly normal plants and plants with undoubtedly enlarged cells was found after treatment with 0,01 % solution (Fig. 2 *i*, *k*). It can be concluded that the brown algae studied either are immune to both colchicine and acenaphthene, the only response being due to a poisonous effect, or their reaction is very slow, only certain cells responding with c-mitoses to 0,01 % colchicine; even

in 0,1 % and in acenaphthene a few mitoses may occur before the action is complete.

DISCUSSION OF THE RESULTS.

It has been shown that the two *Ulva* species react to acenaphthene with a typical c-mitosis. What happens after a prolongated treatment is still unknown, but it is possible that *Ulva* behaves towards acenaphthene in the same manner as higher plants behave towards colchicine.

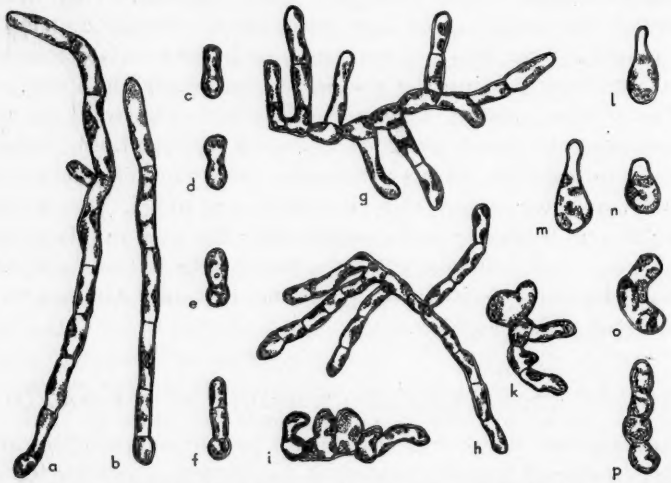

Fig. 2. *a—f*: *Ectocarpus siliculosus*, 10 days, *a*: untreated, *b*: 0,01 % colchicine, *c—f*: 0,1 % colchicine; *g—p*: *Spermatochnus paradoxus*, *g*: untreated, *h—k*: 0,01 % colchicine, *l—p*: 0,1 % colchicine. — × 600.

Its reaction is more complete and more rapid than, for instance, the response of an *Allium* root to acenaphthene. In *Allium* several normal mitoses occur before the action of acenaphthene takes effect. Colchicine, on the other hand, acts very slowly in *Ulva*, if there is any specific action of the colchicine at all. In *Allium* even a treatment of a few minutes with 0,01 % colchicine turns all mitoses into c-mitoses. In *Ulva* 0,01 % had no visible action at all, and 0,1 % permitted mitoses to occur, though at a slower rate. Even 1 % colchicine did not completely suppress the mitotic action. Hence the conditions seem to be reversed in *Ulva* as compared with higher plants, acenaphthene working by far more effectively than colchicine. It should be noted that the same situation has been described in several of the studies on lower organisms,

cited in the introduction of this paper. It should also be recalled that *Colchicum*, although completely immune to colchicine, was extremely sensitive to acenaphthene (LEVAN, 1940).

What can be the cause of this differential behaviour? Several explanations may be suggested, none of them being approachable for a crucial test so far. Differences in the molecular building up of the spindle organs may be present between different groups, the spindle organs of certain plants becoming locked by the colchicine molecule, others not. This view is strengthened by the specific nature of the colchicine action: The characteristic course of the c-mitosis implies a change within some basic factor governing the entire course of mitosis rather than a general poisoning process affecting the whole cell. If this view be correct, there might lie a special interest in the detailed study of the behaviour of different plant groups. Differences in reaction would indicate differences in the organisation of the spindle apparatus, and the study of these differences could give clues concerning the relationships and the phylogeny of plant groups.

The other alternative is that the spindle organs are identical, but that other factors in the cells are responsible for the differences. These factors may be certain differences in the genetic constitution, acting for instance through certain substances which guard the spindle organs so that the colchicine never gets an opportunity of acting on them. There may be antidotes present in the plasm, breaking down the colchicine molecule, or the very metabolism of the cells may seize upon the colchicine and change it into some innocent form. If it were possible to extract a substance from an immune plant and make a sensitive plant immune by treating it with the extracted substance, this alternative could be tested experimentally. Such attempts have failed so far.

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METHODIK ZUR UNTERSCHEIDUNG VON ERBLICHKEITS- UND MILIEUVARIATIONEN MIT HILFE VON ZWILLINGEN

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EINEIIGE Zwillinge besitzen dieselbe Erbmasse, während hingegen zweieiige Zwillinge in grösserem oder geringerem Masse erblich bedingte Verschiedenheiten aufweisen können. Ausgehend hiervon hat man ja bei einer grossen Anzahl von Untersuchungen eineiige und zweieiige Zwillinge zur Entscheidung herangezogen, welche Rolle die Erblichkeit bzw. das Milieu spielt, ferner um eine Vorstellung darüber zu erhalten, inwieweit eine Eigenschaft erblich bedingt ist oder nicht. Man hat sogar über die Zwillingsforschung so gesprochen, als ob sie einen besonderen Zweig der Erblichkeitsforschung darstellen würde. Im Hinblick auf die theoretischen Ausgangspunkte habe ich in früheren Arbeiten (DAHLBERG, 1926 und 1929) geltend gemacht, dass falls es sich um asymmetrische Eigenschaften handelt, eineiige Zwillinge Unterschiede aufweisen können, die erblich bedingt sind. Zahlreiche Autoren haben diesen Standpunkt missverstanden. Man hat bei der Anführung meiner Arbeiten behauptet, dass ich es verneint habe, dass eineiige Zwillinge dieselbe Erbmasse besitzen. Ich will deswegen hier betonen, dass die Theorie über die Vererbung asymmetrischer Eigenschaften, die ich aufgestellt habe, zu dem paradoxen Standpunkt führt, dass eineiige Zwillinge erblich bedingte Verschiedenheiten aufweisen können, obwohl sie dieselbe Erbmasse besitzen. Im Hinblick auf die nähere Ausgestaltung dieses Standpunktes weise ich auf meine früheren Arbeiten hin. Hier will ich nur hervorheben, dass wenn man eineiige Zwillinge als ein gespaltenes Individuum betrachtet, der von mir vertretene Standpunkt kaum schwer zu begreifen ist. Ein Individuum kann auf Grund einer erblich bedingten Asymmetrie ein braunes und ein blaues Auge besitzen. Niemand wird geltend machen wollen, dass die beiden Körperhälften des betreffenden Individuums eine verschiedene Erbmasse besitzen und doch ist der Unterschied erblich bedingt. Analog hierzu kann man sich vorstellen, dass zwei eineiige Zwillinge ausnahmsweise eine verschiedene

Augenfarbe und eine erblich bedingte Verschiedenheit aufweisen, obwohl sie dieselbe Erbmasse besitzen.

Die asymmetrischen Eigenschaften sind, so weit wir jetzt wissen, verhältnismässig selten und die Reservation, die ich angeführt habe, dürfte deswegen in der Praxis keine so grosse Rolle spielen. Man muss sich natürlich immer daran erinnern, dass die Möglichkeit des Vorhandenseins einer asymmetrischen Eigenschaft besteht, wenn man weitgehende Schlüsse zieht, und besonders dann, wenn die gezogenen Schlüsse dem widersprechen, was man auf Grund anderer Untersuchungen berechtigterweise erwarten kann.

Wenn es sich darum handelt eineiige Zwillinge für eine Analyse der Rolle anzuwenden, die Erblichkeits- und Milieufaktoren spielen, so liegen, so weit mir bekannt ist, keine eingehenderen Analysen des Problemes vom mathematisch-statistischen Gesichtspunkt vor. In der vorliegenden Arbeit will ich versuchen eine solche auszuführen.

In einer früheren Arbeit (DAHLBERG, 1926) habe ich hervorgehoben, dass man für die quantitativen Eigenschaften bei Zwillingen die gewöhnliche Formel für den mittleren Fehler einer Differenz und für die Summierung der Dispersionen anwenden kann, um eine Aufteilung des Anteiles auszuführen, den Erblichkeits- und Milieufaktoren für die Entstehung von Unterschieden (z. B. die Körperlänge, den Kopfindex u. s. w.) besitzen.

Bei der Messung der Variabilität bei Zwillingen verwendet man die Formel:

$$\sigma = \pm \sqrt{\frac{\Sigma d^2}{2n}}$$

worin d die Differenzen zwischen den Zwillingspaaren und n die Anzahl Zwillingspaare ausdrückt. Die Standarddeviation, die man so erhält, bezieht sich auf die Variabilität des einzelnen Individuums. Die Formel $\sigma = \pm \sqrt{\frac{\Sigma d^2}{n}}$ vermittelt die Standarddeviation der Differenzen zwischen den Zwillingen. Wenn wir im folgenden von Variabilität sprechen, so hat das Bezug auf die erstgenannte Formel. Wird die Variabilität, die zweieiige Zwillinge aufweisen, durch Vererbung und Milieu bedingt und mit σ_{1+2} bezeichnet und die Variabilität, die bei eineiigen Zwillingen ausschliesslich durch Milieufaktoren bedingt wird, mit σ_1, sowie die Erblichkeitsvariabilität mit σ_2 bezeichnet, so kann man den Wert für die Erblichkeitsvariabilität aus der Gleichung: $\sigma_{1+2} = \sqrt{\sigma_1^2 + \sigma_2^2}$ erhalten. Das Verhältnis zwischen Erblichkeit und Milieu $\sigma_1 : \sigma_2$ wird dann

$\sqrt{\frac{\sigma_1^2 + 2}{\sigma_2^2}} - 1$. LENZ und VERSCHUER (1928) haben angegeben, dass man »den erbbedingten Unterschied der zweieiigen Zwillinge in Bezug auf ein Merkmal dadurch erhält, dass man den Unterschied der eineiigen Zwillinge von dem der zweieiigen Zwillinge subtrahiert». LENZ (1935) hebt hervor, dass diese Behauptung unrichtig ist und gibt als die richtige Methode die Formel an, die ich bereits früher angeführt habe. [LENZ verwendet die durchschnittliche Abweichung anstatt der Standarddeviation, was ja keinen prinzipiellen Unterschied darstellt. Ferner hat VERSCHUER (1926) zwecks Berechnung der durchschnittlichen Differenzen zwischen Zwillingen eine Formel aufgestellt, die er den von GINI angegebenen Konzentrationsmassen entlehnte. (PIZETTI, 1940.)] LENZ ist aber erneut ein Versehen unterlaufen, da er vergessen hat ein Wurzelzeichen einzuführen. Die Werte, die er in einer kleinen Tabelle für das Verhältnis zwischen »Erbmasse» und »Umwelt» angibt, sind deswegen fehlerhaft. Neuerdings hat NEHLS (1941) die fehlerhafte, von LENZ angegebene Formel verwendet, ohne das Übersehen zu beachten, dessen sich LENZ schuldig gemacht hat. Darum wird vor Verwendung dieser Formel gewarnt. LENZ hebt ferner hervor, dass die Variabilität durch Messungsfehler erhöht wird und dass diese »von flüchtigen Unterschieden der Umwelt niemals reinlich zu trennen sind». Dies ist unrichtig. In meiner früheren Arbeit (DAHLBERG, 1926) habe ich durch Doppelbestimmungen Standarddeviationen für den Messungsfehler erhalten. Dieser Messungsfehler kann eliminiert werden. Die Gleichung erhält dann die folgende Form:

$$\sigma_{1+2+3} = \sqrt{\sigma_1^2 + \sigma_2^2 + \sigma_3^2},$$

wobei σ_{1+2+3} die durch Erblichkeit, Milieu und Messungsfehler bedingte Variabilität zweieiiger Zwillinge darstellt. σ_1 ist die wirklich milieubedingte Variabilität der eineiigen Zwillinge, σ_2 die unbekannte wirkliche Erblichkeitsvariabilität und σ_3 der Messungsfehler, der ja bekannt ist. Die von mir angegebene Formel muss aber mit einer gewissen Vorsicht angewandt werden. Man kann das Ergebnis nicht ohne weiteres für Populationen anwenden. Die Erblichkeitsvariabilität, die man bei zweieiigen Zwillingen erhält, ist etwas kleiner als die, welche Bevölkerungen charakterisiert. Man muss sich daran erinnern, dass sich zweieiige Zwillinge durchschnittlich ebenso wie Geschwister, weniger als zwei zufällig aus einer Bevölkerung ausgewählte Personen unterscheiden. Die Möglichkeiten von Zwillingen, sich unterschiedlich zu entwickeln, werden dadurch begrenzt, dass sie dieselben Eltern be-

sitzen. Man kann die Sache so ausdrücken, dass die Erblichkeitsvariabilität, die man erhält, auf der Variabilität beruht, die innerhalb von Familien vorhanden ist und nicht auf der Variabilität, die innerhalb von Bevölkerungen zu finden ist.

Im Hinblick auf die Milieuvariabilität muss man sich daran erinnern, dass die Unterschiede im Milieu, die in einer Familie vorliegen, geringer sind, als die Unterschiede, die für eine Population vorhanden sind. Die Situation ist also die, dass sowohl die Erblichkeits- wie auch die Milieuvariabilität, die man aus einem Zwillingsmaterial

TABELLE 1. *Standarddeviation und Variabilitätskoeffizient für schwedische Rekruten* (LUNDBORG *und* LINDERS, *1926*) *und für Zwillinge* (DAHLBERG, *1926*).

	LUNDBORG und LINDERS		DAHLBERG	
	$\sigma \pm \varepsilon(\sigma)$	v	$\sigma \pm \varepsilon(\sigma)$	v
Kopflänge	6,2 ± 0,02	3,2	5,0 ± 0,4	2,8
Kopfbreite	5,1 ± 0,02	3,4	3,6 ± 0,3	1,6
Frontal. min. Diameter	4,3 ± 0,01	4,1	3,2 ± 0,2	3,3
Gesichtsbreite	4,8 ± 0,02	3,6	3,2 ± 0,2	1,6
Gesichtslänge	6,9 ± 0,02	5,5	3,8 ± 0,3	3,4
Mittelwert für die Gesichtsmasse	—	4,0	—	2,5
Gestalt	59,3 ± 0,2	3,4	48,4 ± 3,6	3,3
Höhe der Symphyse	43,0 ± 0,1	4,7	30,1 ± 2,3	4,0
Armlänge	33,4 ± 0,1	4,3	22,7 ± 1,7	3,6
Rumpflänge	24,1 ± 0,1	4,6	18,5 ± 1,4	4,5
Biacromialer Diameter	16,7 ± 0,1	4,2	12,0 ± 0,9	3,9
Bicristaler Diameter	15,2 ± 0,1	5,3	9,2 ± 0,7	3,6
Mittelwert für die Körpermasse	—	4,4	—	3,8

erhält, theoretisch gesehen kleiner sind, verglichen mit denen, die Bevölkerungen auszeichnen. Die Verminderung kann ja die beiden Variationsquellen proportional betreffen, so dass das Verhältnis zwischen ihnen nicht gestört wird. Dies muss aber nicht notwendigerweise das Verhalten sein; wie gross der Variabilitätsunterschied zwischen Familien und Populationen ist, muss deswegen für jede einzelne Eigenschaft entschieden werden.

Für einige anthropologische Masse hat Verf. früher ein- und zweieiige Zwillinge angewandt um die Rolle, welche Erblichkeit und Milieu spielen, mathematisch zu bestimmen (DAHLBERG, 1926), sowie ferner

berechnet, eine wie grosse Variabilität man bei der Population zu erwarten hat, aus welcher die Zwillinge genommen wurden, und zwar unter der Voraussetzung, dass die Erblichkeits- und Milieuvariabilität für die Zwillinge ebenso gross ist wie für die betreffende Population. Später wurden zahlenmässige Angaben über die Population von Schweden veröffentlicht (LUNDBORG und LINDERS, 1926), so dass es jetzt möglich ist durch einen Vergleich eine Vorstellung darüber zu erhalten, in welchem Ausmasse die oben gemachte Annahme falsch ist. Die Zahlen werden in Tabelle 1 wiedergegeben.

Diese Zahlen ergeben, dass der Variationskoeffizient für die Gesichtsmasse einer Population im Durchschnitt 4 % und der aus Zwillingen berechnete 2,5 % beträgt. Für die Körpermasse sind die durchschnittlichen entsprechenden Werte 4,4 % und 3,8 %. Es soll daran erinnert werden, dass früher ein Vergleich zwischen zweieiigen Zwillingen und Brüdern, die nicht Zwillinge waren und gemessen wurden, als sie ihre Militärdienstzeit machten, also beide 21 Jahre alt waren, angestellt wurde. Die Messungen wurden in zwei aufeinander folgenden Jahren ausgeführt. Die Brüder und die zweieiigen Zwillinge zeigten im Hinblick auf die durchschnittlichen Differenzen keinen Unterschied. Die Verminderung in der Variabilität, die dadurch bedingt wird, dass zweieiige Zwillinge ebenso wie Geschwister im allgemeinen eine geringere Erblichkeitsvariabilität und geringere Milieuvariabilität als die Bevölkerung insgesamt aufweisen, ist also bezüglich der anthropologischen Masse nicht unbedeutend. Unter solchen Umständen ist es immer noch möglich, dass die Relation zwischen Erblichkeit und Milieu, die auf Grund von Untersuchungen bei eineiigen und zweieiigen Zwillingen berechnet wird, nahezu richtig ist; zu völlig bestimmten Ergebnissen kann man aber nicht gelangen. Es soll daran erinnert werden, dass für anthropologische Masse die Variabilität, die die Erblichkeit allein verursacht, d. h. die man in einer Population erhalten würde, in welcher die Erblichkeitsfaktoren wie bei zweieiigen Zwillingen variieren würden, das Milieu aber dasselbe wäre und dem durchschnittlichen bei zweieiigen Zwillingen entsprechen würde, ungefähr zweimal so gross wie die Variabilität ist, welche man ausgehend von eineiigen Zwillingen für eine Population berechnen kann, die die gleiche Erblichkeit besitzt und für welche das Milieu in gleichem Ausmasse wie für eineiige Zwillinge variiert.

Um sich über die Bedeutung der oben angegebenen Formel zu orientieren, werden in Fig. 1 und Tabelle 2 Werte für die Milieuvariabilität bei verschiedenen Werten der Erblichkeitsvariabilität oder um-

gekehrt angegeben. Aus der Tabelle und dem Diagramm ergibt sich, dass z. B. die Erblichkeitsvariabilität bis zu verhältnismässig grossen Werten steigen kann, ohne dass der Unterschied zwischen der nur erblich bedingten Variabilität und der durch Erblichkeit und Milieu

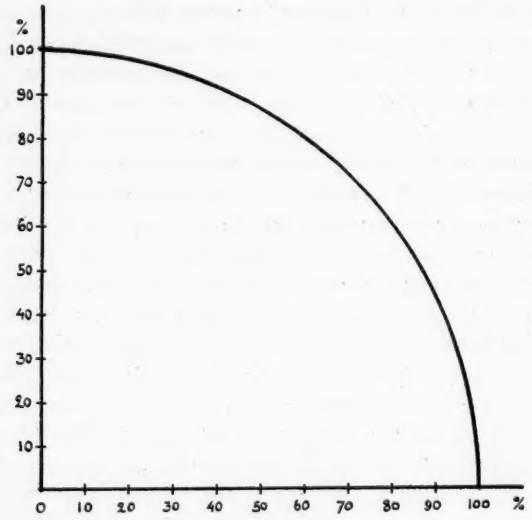

Fig. 1. Werte für σ_1 und σ_2 gemäss der Formel $\sigma_{1+2} = \sqrt{\sigma_1^2 + \sigma_2^2}$.

zusammen bedingten Variabilität gross werden muss. Wenn die Variabilität, die für eineiige Zwillinge bezüglich des Milieus erhalten wird, z. B. 95 % der kombinierten Variabilität beträgt, so findet

TABELLE 2. *Werte für σ_1 und σ_2 gemäss der Formel* $\sigma_{1+2} = \sqrt{\sigma_1^2 + \sigma_2^2}$.

σ_1	0,1	0,2	0,3	0,4	0,5	0,6	0,7	0,8	0,9	1,0
σ_2	0,995	0,980	0,954	0,917	0,866	0,800	0,714	0,600	0,436	0

man bei der Berechnung, dass die Erblichkeitsvariabilität 30 % der kombinierten Variabilität beträgt. Es ist mit anderen Worten von praktischem Interesse, dass wenn auch eineiige und zweieiige Zwillinge einen sehr geringen Unterschied in der Variabilität zeigen, dies doch nicht ausschliesst, dass erbliche Faktoren eine verhältnismässig grosse Rolle

für de Eigenschaften spielen, um die es sich handelt. Um eine exaktere Orientierung zu erhalten, ist ferner ein verhältnismässig grosses Material erforderlich, da zufällige Verschiebungen der Variationsbreite ein- bzw. zweieiiger Zwillinge einen sehr starken Einfluss auf das Ergebnis ausüben.

Durch Berechnung der Korrelationskoeffizienten für eineiige und zweieiige Zwillinge kann man auch eine Vorstellung darüber erhalten, welche Rolle Milieufaktoren im Vergleich zu Erblichkeits- und Milieufaktoren zusammen spielen. Einige Autoren haben diese Methode angewandt, z. B. STOCKS (1930). Man kann natürlich aus den Korrelationskoeffizienten berechnen, welche Korrelation man allein auf Grund von Erblichkeitsfaktoren und unter der Voraussetzung erhalten könnte, dass die Milieufaktoren konstant sind. Indessen geben die Werte, welche man erhalten kann, kein konkretes Bild der Verhältnisse, weswegen die von mir vorgeschlagenen Methoden vorzuziehen sein dürften. Man hat auch die »Variance» (Standarddeviation im Quadrat) dazu angewandt, in Übereinstimmung mit meiner Methode, das Verhältnis zwischen Erblichkeit und Milieu anzugeben (JOHANSSON und HANSSON, 1940). Der Vorteil besteht hierbei darin, dass die Summe der »Variance» für das Milieu und die »Variance» für die Erblichkeit mit der totalen »Variance» übereinstimmt. Die Ungelegenheit besteht auch hier darin, dass die Zahlen keine konkrete Vorstellung vermitteln, weswegen das Vorgehen weniger geeignet sein dürfte.

In der letzteren Zeit hat man immer mehr begonnen das Zwillingsmaterial auch für die qualitativen Eigenschaften anzuwenden. Handelt es sich z. B. darum zu entscheiden, ob eine Krankheit erblich ist oder nicht, so untersucht man eineiige bzw. zweieiige Zwillinge; aus der Konkordanz bzw. Diskordanz, welche die Paare auszeichnet, zieht man Schlüsse. Man geht hierbei davon aus, dass falls eineiige bzw. zweieiige Zwillinge sich auf ungefähr dieselbe Weise verhalten, so spielen Milieufaktoren eine entscheidende Rolle, und wenn grosse Unterschiede zwischen eineiigen und zweieiigen Zwillingen vorliegen, so weist dies darauf hin, dass erbliche Faktoren die Hauptrolle spielen. Es ist wünschenswert das Problem exakter zu lösen.

Man nimmt die Genotypen P_1, P_2, P_3 . . . . P_n mit den Frequenzen p_1, p_2, p_3 . . . . p_n, die sich entsprechend in den Frequenzen a_1, a_2, a_3 . . . . a_n manifestieren, an.

In diesem Falle wird die Frequenz von Paaren, die beide die Eigenschaft haben, für die eineiigen (gleiche Erblichkeit—variierendes Milieu):

$$\Sigma p_i \; a_i^2;$$

für de zweieiigen (variierende Erblichkeit—variierendes Milieu):

$$[\Sigma p_i \; a_i]^2 = \Sigma p_i \; a_i \; \Sigma p_k \; a_k.$$

Die Differenz zwischen ein- und zweieiigen Zwillingen wird also:

$$\Sigma p_i \; a_i \; (a_i - \Sigma p_k \; a_k).$$

Aus der Formel ergibt sich, dass der Unterschied zwischen eineiigen und zweieiigen Zwillingen von der Milieuvariabilität unabhängig ist, die mit sich bringt, dass ein gewisser Genotypus einer mehr oder minder variierenden Frequenz Eigenschaftsträger entspricht. Es ist nur die durchschnittliche Frequenz, die eine Rolle spielt, und die Grösse des Unterschiedes zwischen eineiigen und zweieiigen Zwillingen ist von den Unterschieden abhängig, die in der Frequenz der Eigenschaftsträger oder verschiedener Genotypen vorliegen.

Die Häufigkeit der Eigenschaftsträger beruht natürlich ihrerseits teils auf der Häufigkeit der Erbfaktoren, die eine Rolle spielen, teils auch auf der Häufigkeit der Milieufaktoren, die eventuell für die Entwicklung der Eigenschaft, die man untersuchen will, auch eine Rolle spielen. HOGBEN (1933) hat hervorgehoben, dass die Resultate, die man bei einer Analyse von Erb- und Milieufaktoren erhält, von dem Milieu abhängig bleiben, das die Bevölkerung karakterisiert. LENZ (1939) hat darauf hingewiesen, dass auch die Erbbeschaffenheit der Bevölkerung bezüglich der Häufigkeit jener Anlagen, die man untersuchen will, eine Rolle spielt. Man hat sich indessen mit dem prinzipiellen Hinweis begnügt und das Problem keiner genaueren Analyse unterworfen.

Um die Bedeutung der Formel näher zu beleuchten soll über zwei Spezialfälle berichtet werden.

1) Wir nehmen an, dass in einer Bevölkerung nur zwei verschiedene Genotypen (monohybride Dominanz) vorhanden sind und dass der eine Genotypus die Frequenz p besitzt, was Eigenschaftsträger mit der Frequenz a_1 ergibt, sowie dass der andere Genotypus die Frequenz q aufweist und Eigenschaftsträger mit einer Frequenz von a_2 hervorbringt.

Unter den eineiigen Zwillingen erhält man dann Paare, die beide die Eigenschaft mit einer Frequenz von $pa_1^2 + qa_2^2$ besitzen.

Unter zweieiigen Zwillingen erhält man Paare, die beide die Eigenschaft mit einer Frequenz von $(pa_1 + qa_2)^2$ haben.

(Man nimmt hierbei an, dass die zweieiigen Zwillinge eine gleichgrosse Erblichkeitsvariabilität aufweisen, wie sie die Bevölkerung auf-

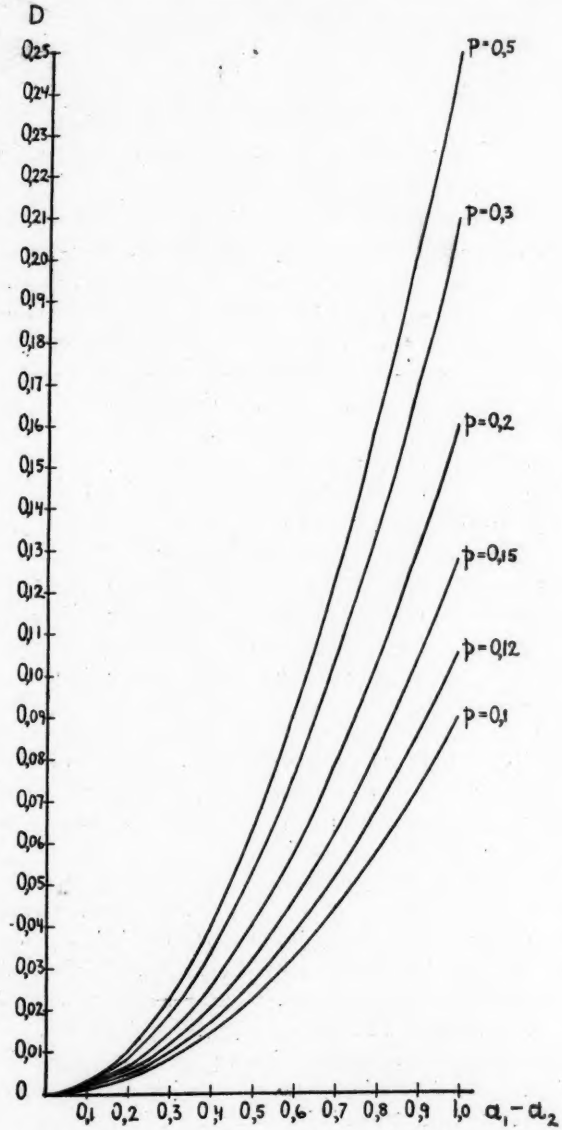

Fig. 2. Werte für Funktion $D = pq\,(a_1 - a_2)^2$ bei variierenden Werten für p und $(a_1 - a_2)$.

weist, was ja kaum der Fall sein dürfte, vgl. weiter oben.) Der Unterschied D zwischen eineiigen und zweieiigen Zwillingen wird:

$$D = pq\,(a_1 - a_2)^2.$$

Der Ausdruck bedeutet, dass die Grösse der Differenz, die man erhält, auf der Frequenz der Genotypen beruht. Der Ausdruck erreicht das Maximum für bestimmte Werte von a_1 und a_2, wenn $p = q = {}^1/_2$, d. h. wenn die beiden Genotypen gleich häufig vorkommen. Die Differenz zwischen eineiigen und zweieiigen Zwillingen nähert sich 0, wenn

TABELLE 3. *Werte für Funktion* $D = pq\,(a_1 - a_2)^2$ *bei variierenden Werten für* p *und* $(a_1 - a_2)$.

$a_1 - a_2$	$p = 0{,}1$	$p = 0{,}12$	$p = 0{,}15$	$p = 0{,}2$	$p = 0{,}3$	$p = 0{,}5$
0,1	0,0009	0,0011	0,0013	0,0016	0,0021	0,0025
0,2	0,0036	0,0042	0,0051	0,0064	0,0084	0,0100
0,3	0,0081	0,0095	0,0115	0,0144	0,0189	0,0225
0,4	0,0144	0,0169	0,0204	0,0256	0,0336	0,0400
0,5	0,0225	0,0264	0,0319	0,0400	0,0525	0,0625
0,6	0,0324	0,0380	0,0459	0,0576	0,0756	0,0900
0,7	0,0441	0,0517	0,0625	0,0784	0,1029	0,1225
0,8	0,0576	0,0676	0,0816	0,1024	0,1344	0,1600
0,9	0,0729	0,0855	0,1033	0,1296	0,1701	0,2025
1,0	0,0900	0,1056	0,1275	0,1600	0,2100	0,2500

p oder q sich 0 nähern. In dieser Situation ist ja praktisch genommen nur der eine Genotypus in der Bevölkerung vorhanden, und die eineiigen und zweieiigen Zwillinge verhalten sich dann gleich. Der Unterschied zwischen eineiigen und zweieiigen Zwillingen ist ferner von dem Unterschied abhängig, der zwischen a_1 und a_2 vorliegt, d. h. von den Unterschieden in der Manifestationsfrequenz der Eigenschaft bei den beiden Genotypen. Liegt hierbei kein Unterschied vor, d. h. wenn $a_1 = a_2$, so ist natürlich zwischen den eineiigen und zweieiigen Zwillingen kein Unterschied vorhanden: je grösser die Manifestationsunterschiede sind, um so grösser fallen die Unterschiede aus. Fig. 2 und Tabelle 3 geben Kurven wieder, die mit Hilfe dieses Ausdruckes berechnet sind. Aus dem Diagramm ergibt sich, dass verhältnismässig grosse Manifestationsunterschiede vorliegen können, ohne dass man grössere Unterschiede zwischen den eineiigen und zweieiigen Zwillingen erhält. Ist z. B. der eine Genotypus bei 50 % der Bevölkerung vor-

handen, und manifestiert sich die Eigenschaft immer bei diesem Genotypus, und hat der andere Genotypus ebenfalls eine Frequenz von 50 %, manifestiert sich die Eigenschaft bei ihm aber nur bei der Hälfte derjenigen, die den Genotypus besitzen, so wird der Unterschied zwischen den eineiigen und zweieiigen Zwillingen 6,25 %. (Unter eineiigen Zwillingen finden sich, gemäss der oben angegebenen Formel, 62,50 % Paare, bei welchen beide die Eigenschaft aufweisen und 56,25 % unter den zweieiigen Zwillingen.) Wenn $p = 10$ %, so ist der maximale Frequenzunterschied von Paaren, bei welchen beide die Eigenschaft aufweisen, 9 % (d. h. wenn alle mit einer Anlage die Eigenschaft haben, und alle mit der anderen Anlage die Eigenschaft nicht besitzen). Aus dem Diagramm kann mit anderen Worten abgelesen werden, dass erbliche Faktoren von wesentlicher Bedeutung für die Entstehung einer Eigenschaft sein können, ohne dass der Unterschied zwischen eineiigen und zweieiigen Zwillingen sehr gross sein muss, ein Ergebnis, das ja mit dem übereinstimmt, was im Hinblick auf die quantitativen Eigenschaften bemerkt werden konnte. Der Spezialfall, den wir hier besprechen, bezieht sich auf solche Eigenschaften, die teilweise erblich und teilweise milieubedingt sind, wo man aber von einer verschieden erblichen Disposition für gewisse Eigenschaften in einer Bevölkerung sprechen kann.

2) Man geht einen Schritt weiter und nimmt an, dass eine Eigenschaft mit einer gewissen Frequenz p_1 auf erblichen Faktoren und eine andere p_2 auf Milieufaktoren beruht. Eineiige Zwillinge werden dann beide die Eigenschaft in $p_1 + p_2^2 - p_1 p_2^2$ Fällen aufweisen. Zweieiige Zwillinge haben beide die Eigenschaft in einer Frequenz $(p_1 + p_2 - p_1 p_2)^2$. Der Unterschied in der Frequenz zwischen eineiigen und zweieiigen Zwillingen wird $D = p_1 \ (1 - p_1)(1 - p_2)^2$. Der Unterschied beruht auch hier auf der Frequenz der Anlage und erreicht einen gewissen Maximalwert für p_2 wenn $p_1 = {}^1/_2$, d. h. wenn die Eigenschaft bei der Hälfte der Bevölkerung durch Veranlagung bedingt ist.

Aus Fig. 3 und Tabelle 4 wird eine Orientierung über die Werte erhalten, die man bei verschiedenen Frequenzen von p_1 und p_2 erhält. Ist p_1 0,5, so ist der höchste Wert, den man erhält 25 %, wobei p_2 0 ist, d. h. die Eigenschaft wird nicht durch Milieufaktoren bedingt und kommt also als erblich bei der Hälfte der Bevölkerung vor. Besitzt die Anlage die Frequenz ${}^1/_2$ und die Milieufaktoren die Frequenz ${}^1/_2$, so wird die Differenz der Frequenzen zwischen ein- und zweieiigen Zwillingen ${}^1/_{16}$ betragen, d. h. 6,25 %. Man muss sich daran erinnern, dass wenn das Milieu und die Vererbung in der Population je eine Frequenz von ${}^1/_2$ haben, so werden einige Individuen die Eigenschaft sowohl auf

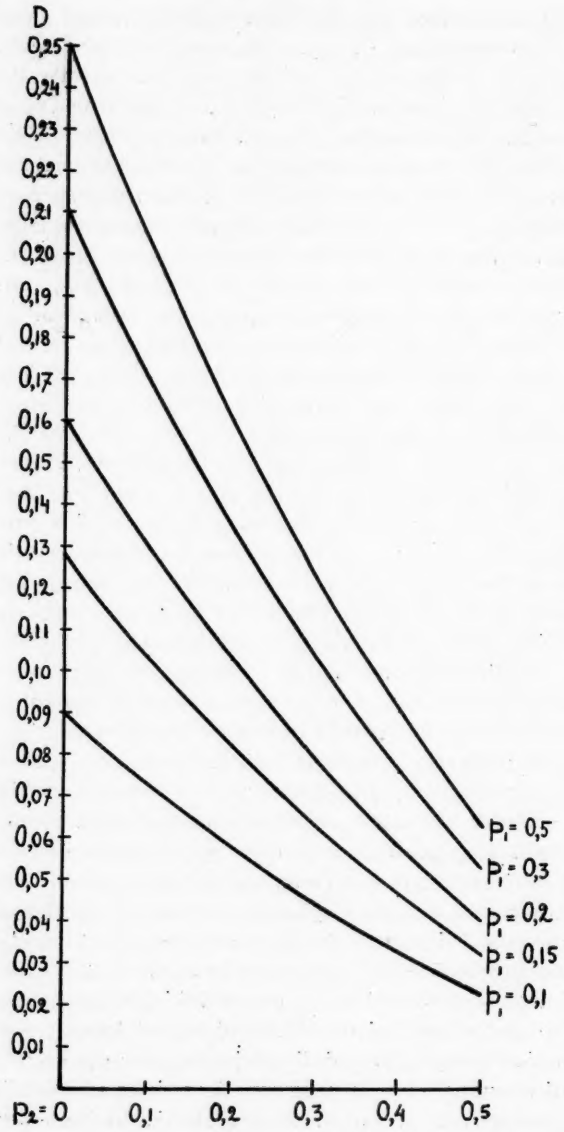

Fig. 3. Werte der Funktion $D = p_1 (1 - p_1)(1 - p_2)^2$ bei variierenden Werten für p_1 und p_2.

Grund der Vererbung wie auch des Milieus besitzen und einige werden überhaupt nicht den beiden Faktoren ausgesetzt sein. Erst wenn die Milieufaktoren eine Frequenz von 1 haben und bei der ganzen Bevölkerung vorkommen, verschwindet der Unterschied zwischen ein- und zweieiigen Zwillingen vollständig. Aus der Formel und dem Diagramm geht nun hervor, dass die Differenzen maximal 25 % erreichen können und dass bei kleinen Differenzen von 5 und 10 % grosse Unterschiede in der Frequenz zwischen Erblichkeits- und Milieufaktoren vorliegen können. Beträgt der Unterschied z. B. 5 %, so kann die Eigenschaft in 10 % erblich und in 25 % milieubedingt sein. Die Eigenschaft kann indessen auch in 20 % erblich und in 44,5 % milieubedingt sein. Ein

TABELLE 4. *Werte der Funktion* $D = p_1(1 - p_1)(1 - p_2)^2$ *bei variierenden Werten für* p_1 *und* p_2.

p_1 \ p_2	0	0,1	0,15	0,2	0,3	0,4	0,5
0,1	0,0900	0,0729	0,0650	0,0576	0,0441	0,0324	0,0225
0,15	0,1275	0,1033	0,0921	0,0816	0,0625	0,0459	0,0319
0,2	0,1600	0,1296	0,1156	0,1024	0,0784	0,0576	0,0400
0,3	0,2100	0,1701	0,1517	0,1344	0,1029	0,0756	0,0525
0,4	0,2400	0,1944	0,1734	0,1536	0,1176	0,0864	0,0600
0,5	0,2500	0,2025	0,1807	0,1600	0,1225	0,0900	0,0625

kleiner Unterschied zwischen ein- und zweieiigen Zwillingen schliesst immer noch nicht aus, dass erbliche Faktoren verglichen mit Milieufaktoren eine nicht unwesentliche Rolle spielen.

Wie weiter oben hervorgehoben, untersucht man, wenn es sich um qualitative Eigenschaften handelt, wie viele Paare konkordant sind und wieviele diskordant. Wenn eine bestimmte Eigenschaft mit einer gewissen Wahrscheinlichkeit bei einem Teil der Zwillinge vorkommt, werden wir teils Paare erhalten, die beide die betreffende Eigenschaft haben und teils Paare, in welchen nur der eine die Eigenschaft aufweist, teils endlich Paare, in welchen beide die Eigenschaft vermissen lassen. Die letztgenannte Gruppe kann nicht von der Gruppe von Zwillingen abgetrennt werden, für welche keine Wahrscheinlichkeit vorliegt, dass die Eigenschaft auftreten soll. Bei qualitativen Eigenschaften er-

hält man unter allen Umständen eine Auswahl von Paaren, bei welchen die Eigenschaft bei wenigstens einem Paarling auftritt, und zwar auf dieselbe Weise, wie man bei der Beschaffung von Angaben über Geschwisterscharen, wenn es sich um qualitative Eigenschaften handelt, immer eine Auswahl von solchen Geschwisterscharen erhält, in welchen wenigstens eines der Mitglieder die Eigenschaft aufweist. Handelt es sich um quantitative Eigenschaften, so besteht das Risiko eines Auswahlmomentes desselben Typus nicht.

Um bezüglich qualitativer Eigenschaften das Auswahlmoment auszuschliessen, wendet man dieselben Methoden an, wie wenn es sich um Geschwisterscharen handelt. Hierbei liegen zwei Möglichkeiten vor.

1) Man hat alle Zwillinge in einer bestimmten Population untersucht. In diesem Falle ist es ja leicht aus dem Verhältnis zwischen konkordanten und diskordanten Paaren die Anzahl konkordanter Paare zu berechnen, bei denen die Eigenschaft fehlt. Die konkordanten Paare K werden $= 2a^2$, die diskordanten Paare $DK = 2ab$ gesetzt. Nachdem man b berechnet hat, erhält man die Anzahl konkordanter Paare, bei denen die Eigenschaft fehlt, durch Berechnung von b^2. Dies ist ja im Prinzip dasselbe Vorgehen wie für Geschwisterscharen, die zwei Mitglieder umfassen, nach der Geschwistermethode von WEINBERG.

2) Innerhalb einer bestimmten Population ist man von Zwillingen ausgegangen, welche die Eigenschaft gezeigt haben und hat sekundär die Zwillinge Nr. 2 berücksichtigt. Man muss hierbei sorgfältig unterscheiden zwischen Probanden, von denen man ausgegangen ist und welche beide in einem Paar darstellen können oder nur den einen, sowie den Zwillingen, über welche man sich sekundär Angaben verschafft hat. In diesem Falle muss beachtet werden, dass Paare, in welchen beide die Eigenschaft haben, eine doppelt so grosse Aussicht haben Probanden zu werden als Paare, von welchen nur der eine die Eigenschaft besitzt. Paare, in welchen bei beiden die Eigenschaft fehlt, können niemals mitkommen. Bei Korrektion der Zahlen verdoppelt man die Anzahl konkordanter Paare, in welchen beide Probanden sind und führt dann dieselbe Korrektion wie oben durch. Das Vorgehen bedeutet im Prinzip, dass man analog zur Probandenmethode von WEINBERG korrigiert.

Eine Schwierigkeit, wenn man die Zahlen bewerten soll, die man aus einem Zwillingsmaterial erhalten hat, ist, dass die Eigenschaft, die man untersucht, vielleicht erst in einem gewissen Alter auftritt und hierbei eine gewisse Variation aufweist. Es kann sich um eine Krankheit handeln, die sich im Erwachsenenalter äussert. Die Ergebnisse, die erhalten werden, sind teils von der Altersverteilung, die das Material

aufweist, teils von der Beobachtungszeit, die vorliegt, abhängig. Untersucht man eineiige und zweieiige Zwillinge im selben Alter und ist die Beobachtungszeit für beide Gruppen gleich gross, so gelten die Zahlen, die man erhält, für das betreffende Alter und die Beobachtungszeit.

Es ist ja offenbar, wenn man z. B. beabsichtigt zu untersuchen, in welchem Ausmasse der Zahnwechsel auf eine durch erbliche Faktoren bestimmte Weise vor sich geht und hierzu Zwillinge anwendet, dass das Ergebnis davon abhängig wird, welches Alter man für die Untersuchung wählt. Sind die Zwillinge zu jung oder zu alt, so erhält man natürlich keinen Unterschied zwischen eineiigen und zweieiigen Zwillingen, nachdem der Zahnwechsel entweder noch nicht begonnen hat oder abgeschlossen ist. Wie gross die Unterschiede sind, die man erhält, beruht darauf, welches Alter man wählt und wird ferner dadurch bestimmt, ob man in einem bestimmten Alter eine Beobachtung macht oder die Zwillinge wiederholt untersucht. In der Regel dürfte indessen sowohl das Alter wie auch die Beobachtungszeit von Paar zu Paar beträchtlich schwanken und das Material, aus eineiigen bzw. zweieiigen Zwillingen bestehend, kann Verschiedenheiten aufweisen. Ein Unterschied zwischen den Zwillingen kann entweder durch Altersverschiedenheiten oder Verschiedenheiten in der Beobachtungszeit oder beide bedingt werden. Offenbar erhält man in der Regel bezüglich Krankheiten eine höhere Frequenz bei dem Material, das das höhere Alter erreicht und das man am längsten beobachtet hat. Bei den meisten bisher durchgeführten Untersuchungen hat man dieses Verhalten nicht beachtet und nicht einmal angegeben, eine wie lange Beobachtungszeit vorgelegen hat.

Untersucht man z. B. das Auftreten von Geisteskrankheiten bei Zwillingen, so sind die Zahlen, die man erhält, vom Alter und der Beobachtungsperiode abhängig. Gewissermassen fällt das Alter mit der Beobachtungszeit zusammen, da man ja damit rechnen kann, dass kaum Fälle mit vorübergehender Geisteskrankheit übersehen werden. Wenn nun in zahlreichen Fällen nur der eine erkrankt, muss man, um das Ergebnis bewerten zu können, berücksichtigen eine wie lange Zeit zwischen dem Zeitpunkt des Erkrankens des ersteren und dem Abschluss der Beobachtungszeit vergangen ist. Wenn der erste im allgemeinen unmittelbar vor der Vornahme der Untersuchung erkrankte, so ist die Aussicht auf eine Diskordanz grösser, als wenn eine längere Zeit verstrichen ist. Wenn auch die Geisteskrankheiten in einem wesentlichen Grade erblich bedingt sind, kann man ja nicht erwarten, dass die beiden Zwillinge in einem Paar präzis gleichzeitig erkranken werden. Man

muss in erster Linie eine Vorstellung über die durchschnittliche Zeit geben, die von der frühesten Erkrankung bis zum Abschluss der Untersuchung vergangen ist.

In gewissen Untersuchungen hat man ein von WEINBERG angegebenes approximatives Verfahren angewandt, bei welchem man eine gewisse Risikoperiode abgrenzt (Gefährdungsperiode) und die Individuen, welche die obere Grenze der Periode nicht erreicht haben, als halbe rechnet. Die Methode ergibt unter der Voraussetzung richtige Werte, dass man eine Risikoperiode richtig abgrenzen kann und dass das Risiko sich während dieser auf eine symmetrische Weise um einen Mittelwert verändert, sowie dass das Alter und die Beobachtungsperioden der Individuen sich auch symmetrisch um den Mittelwert verteilen. Diese Voraussetzungen dürften in vielen Fällen nicht vorliegen. Handelt es sich z. B. um Krankheiten, so fehlen in den meisten Fällen Risikowerte, die es ermöglichen die Zahlen für eineiige und zweieiige Zwillinge zu vergleichbaren Werten zu korrigieren. Deswegen ist es von Wichtigkeit zu versuchen Material zu erhalten, in welchem die Alterszusammensetzung und die Beobachtungszeit gleich ist. Auch wenn man diese Vorsichtsmassnahmen berücksichtigt, werden die Zahlen, die man erhält, nicht immer leicht zu erklären sein. Man kann sie ja nicht auf Populationen anwenden ohne Risikowerte zu besitzen. Die Unterschiede, welche man zwischen eineiigen und zweieiigen Zwillingen erhält, sind von der Frequenz der Eigenschaft in der Population, aus welcher die Zwillinge genommen wurden, abhängig. Sind nun die Zahlen, die man erhält, auf ein bestimmtes Alter und eine gewisse Beobachtungszeit zurückzuführen, so muss man die Frequenz der Eigenschaft in diesem Alter und dieser Beobachtungszeit kennen, um entscheiden zu können, welche Bedeutung die Unterschiede zwischen eineiigen und zweieiigen Zwillingen haben, wenn man aus diesen berechnen will, eine wie grosse Rolle Erblichkeits- bzw. Milieufaktoren spielen. Ein grosser Teil der klinischen Untersuchungen, die über das Vorkommen von Krankheiten bei Zwillingen ausgeführt wurde, leidet deswegen an grossen Mängeln.

Die Situation ist eine andere, wenn es sich um Eigenschaften handelt, bei denen Alter und Beobachtungszeit eine kleine oder gar keine Rolle spielen. Handelt es sich um die Frequenz angeborener Eigenschaften, wie Missbildungen, Augenfarbe u. s. w., so machen sich diese Schwierigkeiten nicht geltend. In diesem Falle kann man hingegen aus den Zahlen, die man für eineiige und zweieiige Zwillinge erhält, die Frequenz der entsprechenden Eigenschaften in den Bevölkerungen berechnen. Aus einer bei Zwillingen vorkommenden Eigenschaft und der

Häufigkeit mit der diese Eigenschaft in der Bevölkerung vorkommt, kann man bezüglich der Art der Vererbung Schlussfolgerungen ziehen. Man kann entscheiden, ob die Zahlen mit denen übereinstimmen, die man z. B. bei Monohybridität zu erwarten hat. Beim Durchsehen der Literatur zeigte es sich, dass Formeln dieser Art früher von RIFE (1938) angegeben wurden. Hier erscheinen deshalb nur Formeln für monohybride Dominanz und monohybride Regressivität. In diesen Fällen hat

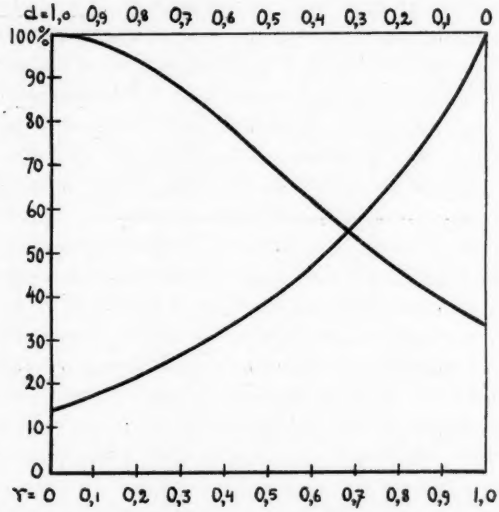

Fig. 4. Verhältnis zwischen konkordanten und konkordanten + diskordanten Paaren bei Rezessivität Q_r gemäss der Formel $Q_r = \frac{(1+r)^2}{7-2r-r^2}$ und bei Dominanz Q_d gemäss der Formel $Q_d = \frac{4+r^2-r^3}{4+7r^2+r^3}$.

man folgende Eigenschaftstypen und folgende Zusammensetzung von Zwillingspaaren zu erwarten. Die rezessive Anlage wird mit r bezeichnet, die dominante mit d (Tabelle 5 und Fig. 4).

Durch Summation der Ausdrücke erhält man für das Verhalten zwischen konkordanten und konkordanten + diskordanten Paaren bei Rezessivität die folgende Formel:

$$Q_r = \frac{(1+r)^2}{7-2r-r^2}.$$

Ist $r = 0$, so wird der Ausdruck $= {}^1/_7$, d. h. ist die Anlage und die

TABELLE 5. *Frequenz von Zwillingspaaren verschiedenen Typus in bezug auf die Frequenz der Eltern verschiedenen Typus bei variierender Frequenz einer rezessiven Anlage r und der entsprechenden dominanten Anlage d.*

Eltern		1 $RR + RR$	2 $RR + RD$	3 $RR + DD$	4 $RD + RD$	5 $RD + DD$	6 $DD + DD$
$RR \times RR$	r^4	r^4					
$RR \times RD$	$4\ r^3d$	r^3d	$2\ r^3d$		r^3d		
$RR \times DD$	$2\ r^2d^2$				$2\ r^2d^2$		
$RD \times RD$	$4\ r^2d^2$	$\frac{1}{4}\ r^2d^2$	r^2d^2	$\frac{1}{2}\ r^2d^2$	r^2d^2	r^2d^2	$\frac{1}{4}\ r^2d^2$
$RD \times DD$	$4\ rd^3$				rd^3	$2\ rd^3$	rd^3
$DD \times DD$	d^4						d^4
Summe		$\frac{1}{4}r^2(1+r)^2$	$r^2(1-r^2)$	$\frac{1}{2}r^2(1-r)^2$	$r(1-r)(1+r-r^2)$	$r(1-r)^2(2-r)$	$\frac{1}{4}(1-r)^2(2-r)$

TABELLE 6. *Verhältnis zwischen konkordanten und konkordanten + diskordanten Paaren bei Rezessivität Q_r gemäss der Formel*

$$Q_r = \frac{(1+r)^2}{7-2r-r^2}$$

und bei Dominanz Q_d gemäss der Formel

$$Q_d = \frac{4+r^2-r^3}{4+7r^2+r^3}.$$

r	0,1	0,2	0,3	0,4	0,5	0,6	0,7	0,8	0,9	1,0
Q_r, %	17,82	21,95	26,78	32,45	39,13	47,06	56,56	68,07	82,23	100,00
Q_d, %	98,48	94,03	87,25	79,01	70,21	61,52	53,35	45,91	39,24	33,33

Eigenschaft sehr selten, so erhält man ein konkordantes Paar auf 7 Paare, von welchen mindestens eines die Eigenschafts besitzt. Wird $r = 1$, so wird der Ausdruck 1, d. h. alle Paare werden konkordant.

Die Werte zwischen diesen Grenzen entsprechen verschiedenen Frequenzen von Anlage und von Eigenschaftsträgern in der Population.

Bei Dominanz erhält man analog für das Verhalten von konkordanten zu konkordanten + diskordanten Paaren:

$$Q_d = \frac{4 + r^2 - r^3}{4 + 7r^2 + r^3}.$$

Wenn die dominante Anlage selten ist, d. h. $r = 1$, ferner $d = 0$, so wird der Ausdruck $^1/_8$, was bedeutet, dass man ein konkordantes Paar gegen 2 diskordante erhält. Ist die Anlage sehr verbreitet, d. h. $r = 0$ und $d = 1$, so wird der Ausdruck 1, d. h. alle Paare sind konkordant. Eine Orientierung über die Zahlen, die man bei verschiedenen Frequenzen erhält, wird in Fig. 4 und Tabelle 6 gegeben.

Es ist natürlich möglich auch in anderen Situationen, z. B. kompliziertere Formen von Erblichkeit oder wenn es sich um Eigenschaftsträger handelt, die teilweise durch Milieufaktoren bedingt werden, teilweise auf Erblichkeitsfaktoren beruhen, die Frequenz der Eigenschaften für eine Population zu berechnen, aus welcher man ein Zwillingsmaterial geholt hat. Für exaktere Berechnungen sind indessen Anhaltspunkte notwendig, die man gegenwärtig nicht erhalten kann, weswegen es kaum von Interesse ist zu versuchen, mathematische Ausdrücke zu erreichen, die für verschiedene Situationen abgepasst sind. Dies um so mehr als das Zwillingsmaterial in der Regel zu klein ist, um bestimmtere Schlüsse über die Frequenzen in Populationen zu erlauben. Wir erinnern indessen daran, dass wir früher, wenn es sich um qualitative Eigenschaften handelt, einen Vergleich zwischen dem Charakter, den man bei der Population erwarten konnte, ausgehend vom Zwillingsmaterial und der faktischen Beschaffenheit der Population haben anstellen können. Der Vergleich hat aber nur zur Aufgabe gehabt, die verminderte Variabilität, die das Zwillingsmaterial im Vergleich zum Populationsmaterial aufweist, zu veranschaulichen.

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A GENE FOR THE REMAINING IN TETRADS OF RIPE POLLEN IN PETUNIA

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IN the course of routine pollen analysis within my *Petunia* material during the autumn of 1938 I came across a number of plants in which the ripe pollen, after the dehiscence of the anthers, still remained hanging together in tetrads. This property was found in 11 among 34 plants of one number, 38—2049. This number constituted the selfed progeny of one white-flowering *Petunia nyctaginiflora* plant which had the same descent as the white-flowering *vv* plants in LEVAN, 1937, and the *nyctaginiflora* plants in LEVAN, 1939 (Scheme 1, p. 153). As only a part of the seed of 38—2049 had been sown in 1938, the rest of it was sown in 1939 together with progenies of six selfed plants of 38—2049. Even at this early point it was realized that the tetrad quality was inherited, plants with tetrad pollen always giving exclusively tetrad plants on selfing, while plants with normal pollen partly gave normal constant progeny and partly segregated in normal and tetrad plants, approximately in the ratio of 3 : 1. It could therefore be assumed that the tetrad quality was determined by a recessive gene, *t*, present in a homozygous condition. Crosses were performed in 1939 in order to test this assumption. About 1000 progeny plants after these crosses were cultivated in 1940. With one or two exceptions, which may be ascribed to experimental errors, all these progenies showed the expected behaviour.

As all the different progenies agreed rather well, I consider it unnecessary to publish the detailed segregation numbers. Only a brief survey of the results will be given. 19 plants in the cross $TT \times TT$, 103 plants in the cross $TT \times Tt$ and 13 plants in the cross $TT \times tt$ all had exclusively normal pollen. 381 plants in the cross $tt \times tt$ had tetrad pollen. The progenies $Tt \times Tt$ and $Tt \times tt$ are recorded in the first two rows of Table 1. As seen from this table they show the expected segregations. No differences were met with between reciprocal crosses.

Within the material there occurred another segregating factor, viz. presence or absence of a black veination in the flower throat. In

contradistinction to other flower veinations this type is called the α-net. The α-net is caused by a dominant gene *A*, and the *aa*-plants lack the α-net. 155 plants of the cross *AA* × *Aa* all had α-net while 25 plants

TABLE 1. *Progenies segregating in the factors T and A.*

Type of cross	Phenotypes				Expected segregation	χ^2
	TA	*Ta*	*tA*	*ta*		
Tt × *Tt*	160	—	53	—	3 : 1	0,0016
Tt × *tt*	155	—	140	—	1 : 1	0,7228
Aa × *Aa*	374	122	—	—	3 : 1	0,0431
Aa × *aa*	126	106	—	—	1 : 1	1,7242
TtAa × *TtAa*	92	22	30	9	9 : 3 : 3 : 1	2,0626
TtAa × *ttAa*	47	15	49	14	3 : 1 : 3 : 1	0,2906
TtAa × *ttaa*	44	34	35	30	1 : 1 : 1 : 1	2,9301

of the cross *aa* × *aa* lacked this property. The result of the crosses *Aa* × *Aa* and *Aa* × *aa* is seen from Table 1, row 3 and 4. In the last

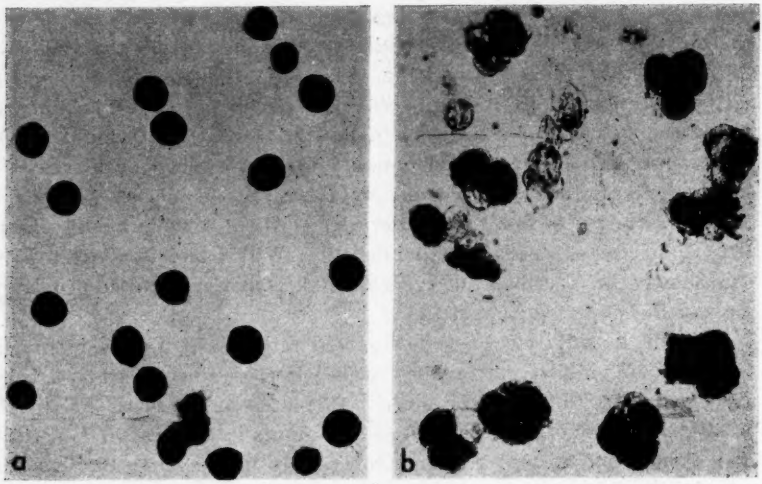

Fig. 1. Microphoto of *a*: normal *Petunia* pollen, *b*: tetrad pollen. — × 125.

three rows of this table there are also collected three types of crosses involving both *T* and *A*. In these cases χ^2 lies between 0,3 and 2,9 (P = 0,30—0,98), so there is no reason to suspect any linkage between *T* and *A*.

The appearance of the tetrad pollen is seen from the microphoto Fig. 1 *b*, while Fig. 1 *a* shows normal pollen at the same developmental stage. The tetrads may be composed of exclusively living pollen grains (Fig. 2 *a*), or 1—4 of the components of each tetrad may be dead (Fig. 2 *b*—*g*). If two grains are dead, they may lie in the same half of the tetrad (Fig. 2 *c*) or opposite each other (Fig. 2 *d*). The appearance of the dead pollen is varying, as is also the case with dead normal pollen grains. If the pollen has died at an early stage it is quite empty and of a smaller size than the typical well-developed grains. Its walls

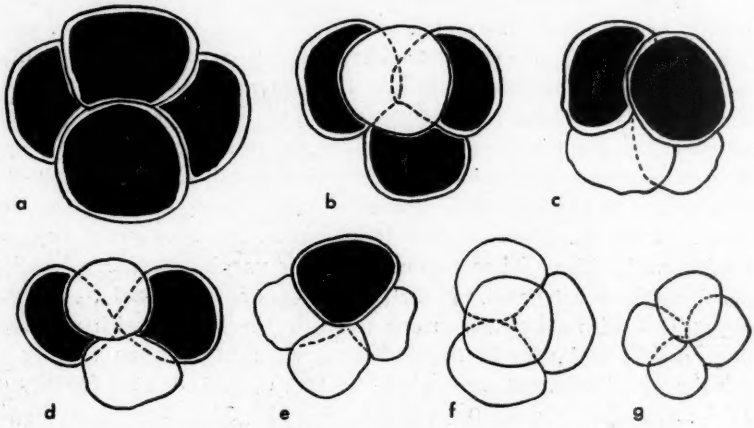

Fig. 2. Different types of pollen tetrads. — × 500.

are then often thin and transparent. All transitions are found from this type to larger pollen grains containing shrivelled dead plasm, darkly stained by aceto-carmine, with thicker and coarser walls, and to normal living pollen grains.

A study of the pollen fertility revealed some interesting facts. Firstly it turned out that the average of families with exclusively tetrad plants had a lower pollen fertility (56,7 %, average of 28 families) than the families with normal pollen (66,8 %, average of 24 families). This difference is also present when the tetrad plants in segregating families are compared with their sister plants with normal pollen. In 18 such families the following differences were determined (pollen fertility of tetrad plants minus that of normal plants):

Difference in %:	— 30	— 20	— 10	± 0	+ 10	+ 20
Number of families:	4	5	4	4	1	

Mean: — 10,78.

Thus, in 13 families the tetrad plants showed decidedly lower fertility, in four families the pollen fertility of the tetrad plants and the normal plants was about the same, and only in one family had the tetrad plants a somewhat better fertility. The average of the whole material showed that the tetrad plants had about 11 % less fertility than the normal plants.

I wished to ascertain whether the *t*-gene in homozygous dose directly brings about this pollen lethality or if specific secondary conditions, caused by the tetrad-property, increased the pollen lethality. In order to elucidate this question I investigated 100 pollen tetrads in each of 49 plants, ranging them in five classes with 0—4 dead pollen grains per tetrad respectively. If the presence of the gene *t* in the genotype is accompanied by a decreased viability of the pollen, the dead pollen grains should be scattered out at random over these five classes in the same manner as, for instance, the number of boys in 4-children families. Expectation curves for varying degrees of pollen sterility were constructed. If the five classes are numbered 1—5, from the class 1 with all pollen grains living to the class 5 with all dead, these curves will vary in the following way: At a pollen fertility of 100 the % of different classes will be 100, 0, 0, 0, 0; at a fertility of 75 %: 31,6, 42,2, 21,1, 4,7, 0,4; at 50 %: 6,3, 25,0, 37,5, 25,0, 6,3; at 25 %: 0,4, 4,7, 21,1, 42,2, 31,6; and at 0 %: 0, 0, 0, 0, 100. At any fertility per cent the random proportions of the classes will be: p^4, $4p^3q$, $6p^2q^2$, $4pq^3$ and q^4, i. e. $(p + q)^4$, where p = the fertility % and $q = 100 - p$.

As an example of the calculations performed the values of one plant are given. Plant No. 2739—3 showed the following frequencies of the different classes:

Class:	1	2	3	4	5
Number of tetrads:	1	2	16	28	53

From this the fertility percentage is determined at 17,5. According to the binomial curve the expected values for this fertility are:

0,1 1,8 12,5 39,3 46,3

The differences between the found and the expected values are:

+ 0,9 + 0,2 + 3,5 — 11,3 + 6,7

In this way 49 series of differences were obtained. The distributions

of all differences of each class are collected in Table 2. From this table it is clearly seen that the dead pollen grains did not occur at random. Instead, there is a great excess in classes 1 and 5, while the classes 2—4 have deficits. It may therefore be concluded that other factors are working than an equal lowering of the viability of all pollen grains, caused by the *tt* condition. The explanation of this may be sought in the organisation of the tetrads. As the class 1 (all pollen grains of the tetrad living) shows a constant excess, the remaining together in tetrads can hardly *per se* be the cause of the increased lethality. In fact, the frequency of class 1 in each separate case is of a magnitude characteristic of a 7—25 (mean 15,9) % higher fertility class. Within this class 1 there occurs, as could be expected, a correlation between the pollen fertility and the deviation from the expected value: the higher the pollen fertility of a plant, the greater the excess of tetrads belonging to class 1.

The intermediate classes 2—4 show an increasing deficit. It may be concluded that the fact that one pollen grain dies within a tetrad predisposes the other pollen grains of the tetrad to die. This tendency is least pronounced in class 2, greater in classes 3 and 4. It

TABLE 2. *The frequency of dead pollen grains in the tetrads (the differences found—expected).*

Tetrad class	−30	−25	−20	−15	−10	−5	±0	+5	+10	+15	+20	+25	+30	Mean
1. All pollen grains of the tetrad living ...	—	—	—	—	—	1	17	20	7	3	1	—		+6,91
2. One dead pollen grain	1	—	1	2	5	15	21	4	—	—	—	—		−1,29
3. Two dead pollen grains	—	2	3	12	15	10	7	—	—	—	—	—		−7,53
4. Three dead pollen grains	—	1	5	15	14	8	5	1	—	—	—	—		−8,78
5. All pollen grains of the tetrad dead ...	—	—	—	—	—	2	7	12	17	9	1	1		+10,69

increases with the increasing number of dead pollen grains in the tetrad. It is close at hand to assume a noxious influence streaming out from the dead component of the tetrad, tending to kill the adjoining pollen grains. Such an influence should work more rapidly within a tetrad in which two or three pollen grains are already dead than in tetrads with only one dead pollen grain. This might explain the greater deficit of classes 3 and 4. The excess present in class 1 is also to be expected according to this view, because the values of class 1 are calculated on the final fertility while in reality they are a function of the original fertility. In normal pollen, where the ripe pollen grains are free, and not in such intimate contact as in these tetrads, the effect of the poison present in the dead pollen grains is of course weaker. Therefore plants with normal pollen should on an average have higher pollen fertility than the tetrad plants, which was also found to be the case.

There are other indications which support the above view. For instance, the pollen of class 1 is often larger and of better development than the pollen of the other classes (Fig. 2 *a* shows a normally developed tetrad of this kind). In tetrads with more than one dead pollen grain it can be seen that the dying has taken place by degrees, first one pollen grain has died at an early stage, after which one or more grains may have atrofied at a more advanced stage, supposedly under the influence of the pollen grain first killed.

It is evident that such a property as this tetrad quality may be extremely valuable and useful for various cyto-genetic experiments. It furnishes an opportunity of studying the four ripe pollen grains which originate from one pollen mother cell. The result of lethality factors, deficiencies, translocations and other meiotic disturbances may be studied directly in the tetrads. In a plant heterozygous for one deficiency all tetrads should contain two living and two dead pollen grains. With the knowledge of the great variety of phenotypes occurring in dying pollen, there should be no difficulty in distinguishing the action of different lethal genes by a mere inspection of the tetrads. The spontaneously occurring lethality will of course be rather disturbing, and therefore lines with only slight spontaneous pollen sterility should be secured. Considerable differences in this respect have been met with.

As I have not yet been able to demonstrate that pollinations with single tetrads can succeed, it is premature to discuss the use of the tetrad quality in the work of factorial analysis. Still, a couple of possibilities may be touched upon: In material homozygous for *tt* but

heterozygous for other factors, a monohybrid segregation might be demonstrated in only four plants. In dihybrid segregations quartets of plants with two plants *AB* and two plants *ab* should occur with the same frequency as quartets of two plants *Ab* and two plants *aB*. If there is linkage between *A* and *B*, an excess of quartets with *AB* and *ab* should be obtained, and so on.

The material has been handed over to Dr. G. HIORTH, Aas, Norway, for a continued examination of the genetical consequences of this pollen anomaly.

I am indebted to Dr. O. TEDIN, Svalöf, for valuable advice.

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NUCLEOLAR CONDITIONS IN PISUM

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IN the course of his studies of various *Pisum* lines the senior author has often noticed the occurrence of certain extra-nuclear bodies during interkinesis. Sometimes even at the first anaphase tiny spherical bodies were observed which were stained both by haematoxylin and gentian violet. In the latter staining they were often of a somewhat paler colour than the chromosomes. These conditions were especially pronounced in one material segregating for the gene *uni* (cf. LAMPRECHT, 1939). The appearance and behaviour of these extra-nuclear bodies is quite in accordance with the findings of FRANKEL (1937) in *Fritillaria*, where small »telophase globules» are present at both meiotic divisions. FRANKEL gave no conclusive decision as to whether these »globules» were of chromatic or nucleolar origin. He seems, however, to lean more to the former alternative (l. c., p. 42).

The presence of extra-nuclear nucleoli has been the subject of considerable discussion (cf. TISCHLER, 1942, p. 200). Often nucleoli have been confused with chromosomes, plastids or precipitations. In almost all cases where true extra-nuclear nucleoli have been met with, it has been a question of persisting nucleoli, i. e. residues of the nucleolus formed at the preceding telophase. As the corpuscles found in *Fritillaria* and *Pisum*, if nucleolar, must belong to the new-started nucleolar cycle and consequently be of a somewhat different nature, a close study of the phenomenon is undoubtedly of great interest. Some old slides of meiosis of various *Pisum* materials earlier studied by HÅKANSSON were re-stained with fuchsine and light green according to SEMMENS and BHADURI (1939). In this technique the chromosomes are stained violet, while nucleolar material is stained green. The stainings, even of rather old slides, were often successful, and it was immediately demonstrated that the extra-nuclear bodies present at interkinesis were nucleoli and not chromosome fragments, since they were stained clearly green. At the same time another interesting condition was encountered. At early interkinesis each of the seven chromosomes formed one separate nucleolus. This has evidently been observed earlier (MARSHAK, 1931), but as no differential staining was

used on that occasion, the writer could not be sure that it was a question of nucleoli: »The regions of spindle fibre attachment in early interphase appear as chromatic globules very much like small nucleoli (Fig. 18)» (MARSHAK, l. c., p. 332). In order to get a fuller picture of the nucleolar cycle also at mitosis root tips were fixed of ten commercial strains of *Pisum sativum* and of one form of *Pisum thebaicum* from the Botanical Garden of Lund. It was found that all these *Pisum* forms behaved similarly; so in the following text they will be treated together.

The mitotic nucleolar cycle. — At late mitotic telophase the first signs of nucleoli may be seen. As at this time the outlines of the chromosomes may still be recognized, it is possible to form an opinion as to what chromosomal part forms the nucleoli. As is seen from Fig. 1 *a—c*, the nucleolar substance appears at first in the distal halves of the two daughter nuclei. In especially favourable cells it is seen that a whole row of nucleoli are formed, although they immediately begin to fuse together. Although it is impossible to indicate the exact point on each chromosome where the nucleoli first appear, it is evident that they are formed in the neighbourhood of the centromeric constrictions. It is often very clear that the two secondary constrictions which are most easily seen in *Pisum*, and which cut off a rather large satellite on the longer arm of one of the largest subterminally constricted chromosomes, have nothing to do with the formation of these nucleoli.

At a somewhat later telophase and early in the resting nucleus the many primary nucleoli have fused into two or three, but most often only one large nucleolus (the latter case occurring in 263 out of 285 studied cells). The percentage of nuclei with more than one nucleolus is higher in some specialized tissues, for instance, in the vascular tissue, where the nuclei are larger and have a more oblong shape. Evidently the chance of all nucleoli fusing into one is greatest in relatively small and spherical nuclei.

The size of the nucleolus is the same during the resting stage and during the early prophase stages. At late prophase it can be seen that the nucleolus is usually situated in the centre of the cell. It may be quite free from contact with any chromosomes, although it is more often attached to one or two chromosomes. Often two short chromosome pieces are attached to the surface of the nucleolus. They might very well be the satellites earlier referred to, but in those cases in which the remaining part of the chromosomes, attached to the

nucleolus, could be followed, it was ascertained that they could *not* be the satellite chromosomes. Instead, these small chromosome pieces were the shorter arms of two chromosomes with subterminal centromeres, and the association between these chromosomes and the nucleolus took place at the centromeric constriction, which is in accordance with the situation of telophase. A close study of late

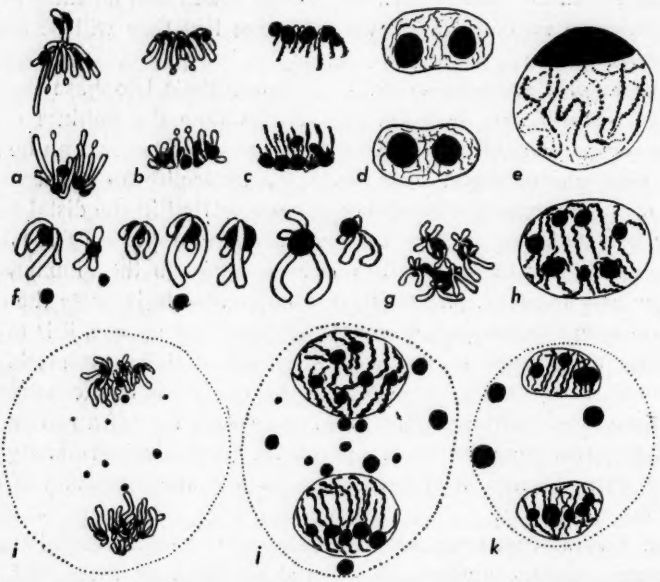

Fig. 1. *a—d*: four consecutive telophase stages of root mitosis. Several nucleoli are formed at the neighbourhood of the centromeres. Note the satellites in *a* and *b*; *e*: pachytene, cap-shaped nucleolus, *f—g*: telophase I, *f*: the seven chromosomes of one telophase group separately drawn, each chromosome forms one nucleolus, in addition three free nucleoli, *h*: interkinesis nucleus showing 7 separate nucleoli, *i*: anaphase I, formation of extra nuclear nucleoli, *j*: interkinesis, many extra-nuclear nucleoli, *k*: ditto, few extra-nuclear nucleoli. — *a—e*, *g—k*: × 1500. *f*: × 3000.

prophase nuclei revealed that small green-stained nucleolar pieces could sometimes occur on other chromosomes than those in contact with the large nucleolus. In some cases these fragments were attached at or near the centromeric region of the chromosomes. This leaves beyond doubt that the situation is the following. At telophase many chromosomes form nucleoli at their centromeric region. These primary nucleoli fuse into one large nucleolus. During this process all chromo-

somes except one or two are torn away from the nucleolus. Small nucleolar fragments may, however, be left on several chromosomes at the original locus of attachment of the nucleolus.

During prophase the nucleolus gradually diminishes, but in many cases it does not disappear when the nuclear membrane dissolves and the chromosomes arrange themselves at the equator. Even at full metaphase a large deeply stained nucleolus very often remains. This persisting nucleolus is very common in Leguminosae, and has been seen in 18 genera (LEVAN, unpublished). It is usually dumb-bell-shaped and one bulb appears at each side of the equatorial plate. In *Pisum*, however, it is ordinarily spherical or irregularly shaped and placed at one side of the plate. At the division of the centromeres in early anaphase every trace of the nucleolus has disappeared.

The meiotic nucleolar cycle. — At meiotic prophase one large nucleolus is present. It undergoes a characteristic development. During early stages in the archesporium and at preleptotene the nucleolus has its ordinary spherical shape. Its diameter is about 4,5 μ. At pachytene it flattens out into a thin layer placed at the surface of the nucleus (Fig. 1 *e*). This »cap-shape» of the nucleolus has been observed on several occasions (cf. FRANKEL, l. c.). Its greatest diameter was determined at 8 μ (mean of 20 measurements). At diakinesis the nucleolus again acquires spherical shape and its diameter is now the same as before pachytene ($\pm$ 4 μ). A close study of many meiotic prophase cells shows that, although one nucleolus is always of dominating size, one or two accessory nucleoli are sometimes present. They are always very small, and are visible only when the green nucleolus stain is strong. Evidently the situation is quite parallel to the conditions of mitotic prophase, where, besides the large nucleolus, small remnants of other nucleoli could be seen in favourable cells. The meiotic nucleolus always disappears completely at the transition to metaphase I, no persisting nucleoli having ever been seen at meiosis.

At telophase I or even sometimes at late anaphase numerous nucleoli begin to appear. Each of the seven chromosomes forms one nucleolus at their centromeric region, and several nucleoli lying free in the plasm may also be seen (Fig. 1 *f*—*k*). The intra-nuclear nucleoli behave broadly speaking as during mitosis. Owing to the low number of chromosomes and the considerable size of the interkinesis nuclei, the pictures are clearer at this stage than during somatic interphase. Immediately after their appearance the seven nucleoli begin to fuse with each other. At an early stage of interkinesis 1—7 (mean 4,1)

nucleoli were counted in 37 cells. At later stages almost all nuclei have only one or two nucleoli.

The extra-nuclear nucleoli which have been observed in exceptional cases, and then only singularly, in root mitoses and at the second telophase, appear almost regularly during interkinesis. Their occurrence is somewhat variable and in some of the investigated plants we only found them in certain cells. In the *uni*-material, on the other hand, there occurred several nucleoli in almost every cell (Fig. 1 *i*, *j*). 3—14 (mean: 8,0) extra-nuclear nucleoli were counted in 30 cells. In other materials there are present very few extra-nuclear nucleoli (Fig. 1 *k*). Each nucleolus is then often larger. In one slide 1—4 (mean: 2,2) nucleoli were counted in 15 cells. The variation within each plant is very considerable, however, so this property is no doubt greatly influenced modificatively.

The extra-nuclear nucleoli show the same developmental rhythm as the ordinary nucleoli. They appear at telophase (Fig. 1 *i*) and are at first very small. They increase in size during interkinesis and disappear before second metaphase. They are probably formed by the chromosomes during their movement from the equator to the poles. The position of equal-sized extra-nuclear nucleoli is often symmetric, indicating that the same pair of separating chromosomes is responsible for their origin. The nucleoli are scattered out most densely in the region between the two interkinesis nuclei, but one or two nucleoli are not infrequently situated at the distal side of the nuclei. The form of some of the large nucleoli shows that they may be the result of fusions of small nucleoli. Fusions are probably rarer, however, than in the intra-nuclear nucleoli, as the number of nucleoli is about the same in late as in early interkinesis.

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A MEIOTIC PECULIARITY IN RYE, SIMULATING A TERMINAL CENTROMERE

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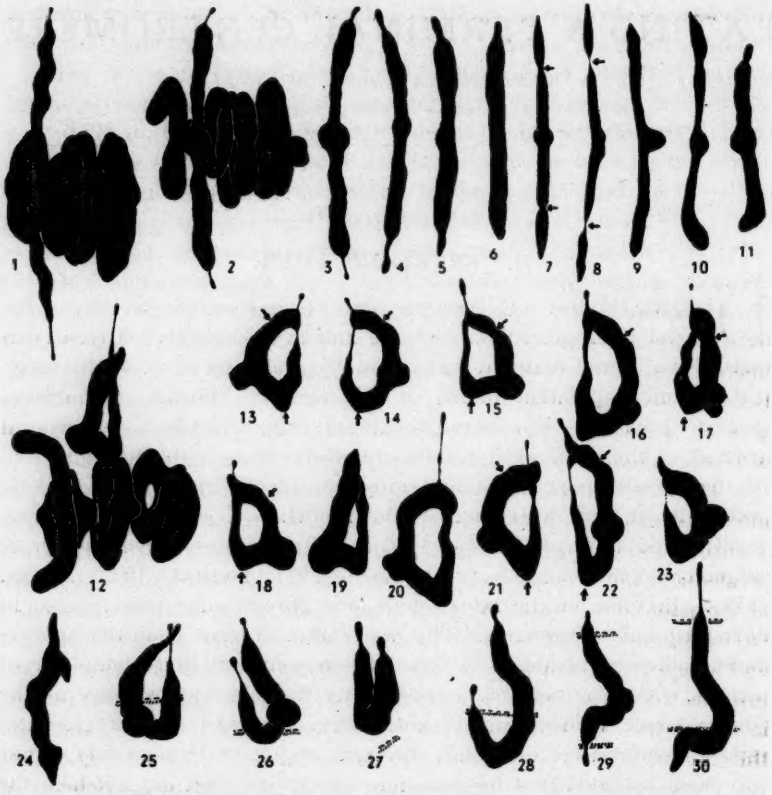
I. INTRODUCTION.

DURING the last few years the writers have studied meiosis in the p. m. c. of inbred lines of rye and in F_1 hybrids between such lines. The inbred material was originally raised by Prof. H. NILSSON-EHLE from population plants of the variety »Stålråg». The lines studied by us had been inbred for about 15 generations. — A general account of the cytological results obtained will be published later on. In the present paper we shall only consider a remarkable meiotic peculiarity, which deserves a special report.

In population plants of rye all the chromosomes have median or submedian centromeres (cf. LEWITSKY, 1931; PATHAK, 1940; LEVAN, 1942). In some of the inbred lines one chromosome pair seemed to have terminal centromeres. This was rather obvious from the appearance of the rod bivalents of these chromosomes at first metaphase of meiosis. At this stage they had exactly the same appearance as the chromosomes with terminal centromeres observed by KATTERMANN (1939) in inbred rye of a quite different origin. A closer study of our case soon revealed that the chromosomes in question did not lack the ordinary submedian centromere. Thus, judging from the meiotic behaviour, they seemed to carry two centromeres, one terminal and one submedian. This remarkable possibility induced us to undertake a close study of meiosis in several lines and also in F_1 hybrids between these lines. This study led to the conclusion that the chromosome ends in question have not an ordinary centromere, though they react in quite a special way. This reaction is probably in part due to a structural differentiation but is also influenced by the genotypic constitution of the lines and F_1 hybrids. Our observations also show that forces of *attraction* between the poles and the special chromosome ends are at work during meiosis in this material.

The observations are based on ears fixed in the summers of 1939—1941, the fixative used being diluted chrome-acetic-formalin. The



Figs. 1—30. First metaphase in plants having a T-chromosome pair. Figs. 1—2, complete groups with one T-rod bivalent and six ordinary bivalents; Figs. 3—11, separate T-rod bivalents. In Figs. 1—3 typical T-rods with small »satellites» on thin threads (taken from the »high-intensity» line 129); Figs. 4—6, less pronounced T-rods from line 175 (»medium intensity»); Figs. 7—9, T-rods from an F_1 plant 128 × 129 (strong differentiation, position of centromeres indicated with arrows); Figs. 10—11, exceptional cases of apparently heteromorphic rod bivalents (from 128 × 129 and line 175 respectively); Fig. 12, a complete I-M group, comprising a T-ring bivalent with its peculiar orientation and position; Figs. 13—24, separate T-rings. In most of the figures 13—24, the two centromeres are indicated with arrows. (Figs. 12—24 were taken from various lines and F_1 combinations. Line 128 is represented by Fig. 18, line 129 by Figs. 13 and 17, line 175 by Fig. 19, 128 × 129 by Figs. 15 and 24, 129 × 175 or reciprocally by Figs. 12, 14, 16, 20—22, and 129 × 143 by Fig. 23.) Figs. 25—30. Transitions between T-rings and T-rods; no chiasmata in the short arms. The double dotted line in Figs. 25—28 indicates the upper contour of the rest of the metaphase group; in Figs. 29—30 both the upper and lower contours are indicated. (Line 128: Fig. 30; line 175: Figs. 27—29; 129 × 143 or reciprocally: Figs. 25—26.) — × 3100.

spikelets were cut at a thickness of about 16 μ, and the slides were stained with gentian violet.

II. TYPICAL BEHAVIOUR OF THE T-CHROMOSOMES AT MEIOSIS.

1. FIRST METAPHASE.

Using the same denomination as KATTERMANN (1939) the peculiar chromosomes in question may be called T-chromosomes (»terminal» chromosomes). They were observed in four inbred lines and in F_1 hybrids involving these lines. The behaviour of the T-chromosomes at meiosis was somewhat different in the various categories of material. Before discussing these differences, however, it may be convenient to give an account of the typical appearance of the T-chromosomes at different stages of meiosis.

The T-chromosomes could not be distinguished at prophase, first metaphase being the first stage at which they are visible. At I-M the T-chromosomes may either be present as rod or ring bivalents. As rod bivalents (Figs. 1—9) they are often easy to distinguish, the members of the pair being stretched towards the poles. Owing to this apparent stretching the chromosomes of the T-bivalents are generally thinner and longer than in other rod bivalents. Further, the free ends, directed towards the poles, are either more or less sharply pointed or drawn out into a satellite-like body, connected with the chromosomes by a generally thin thread. The whole picture strongly suggests an attraction between the chromosome end and the pole. Figs. 1—2 show complete I-M groups with the T-chromosomes as rod bivalents. In Fig. 1 the contrast is very marked between the ordinary bivalents and the long and thin T-chromosomes with their apparent satellites. Figs. 2 and 3 (taken from the same line, 129, as Fig. 1) represent less extreme cases, in which the T-chromosomes may nevertheless be easily distinguished. In Figs. 4—6 (taken from line 175) the satellites are a little larger and less clearly separated from the chromosomes. Especially Figs. 5 and 6 only slightly display the T-chromosome characteristics, and, thus, it is sometimes not possible to distinguish with certainty between T-bivalents and ordinary rod bivalents. This is also demonstrated by the exceptional cases in Figs. 10—11, in which only one member of the bivalent appears to be a T-chromosome. The absence of visible satellites in Figs. 7—10 may be due to a rather intense differentiation of this

particular slide. This strong differentiation may also be responsible for the appearance of clear constrictions in Figs. 7, 8 and 10. These constrictions probably correspond to the position of the centromere. Thus, the chromosome in question consists of a long and a short arm, and it is the end of the latter which shows attraction to the pole. This became quite clear from a study of later stages.

At first metaphase the T-chromosomes may also form closed ring bivalents or apparent rings, in which the free ends lie in close proximity. In good slides the T-rings may be rather easily recognized, partly by the »satellites», partly by a characteristic asymmetrical appearance (Figs. 12—24). In most of these figures the position of the two real centromeres is indicated with arrows. One side of the ring is rather thin and attenuated and often seems to be continued by the thin thread carrying the apparent satellite. This attenuated part represents the smaller arm of one of the chromosomes. Evidently it is stretched as a result of the normal centromere in this chromosome working in a direction more or less opposite to the terminal polar attraction. On the way to the »satellite» this thin, »short», arm is generally attached to the short arm of the other chromosome, which appears to be broad and flattened. The centromere of this chromosome (the position of which is often visible as a slight constriction) and the terminal attraction work in the same direction and mainly therefore the short arm of this chromosome is not attenuated. The long arms of the two chromosomes are usually united by one subterminal or by two chiasmata. In the ring the two arms of the one chromosome are evidently rather sharply bent at the centromere, whereas those of the other one are nearly in line.

Serious efforts were made to find rings in which the mode of connection between the short arms and the course of the chromatids could be studied accurately, but these efforts were not very successful. Usually the attachment between the stretched and the flattened short arms seems to be terminal; in other cases it seems to be subterminal (Figs. 12 and 18) and sometimes it is difficult to decide whether there is any connection at all (Figs. 20—21). In most cases it is impossible to state with certainty to which chromatid the »satellite» belongs and whether it belongs to one or more of the four chromatids. In Fig. 22 the course of the chromatids is rather clear. One of the chromatids of the flattened short arm is directed and stretched towards the pole, the other one is terminally connected with the thin arm of the other chromosome. This bivalent is probably just commencing the anaphase

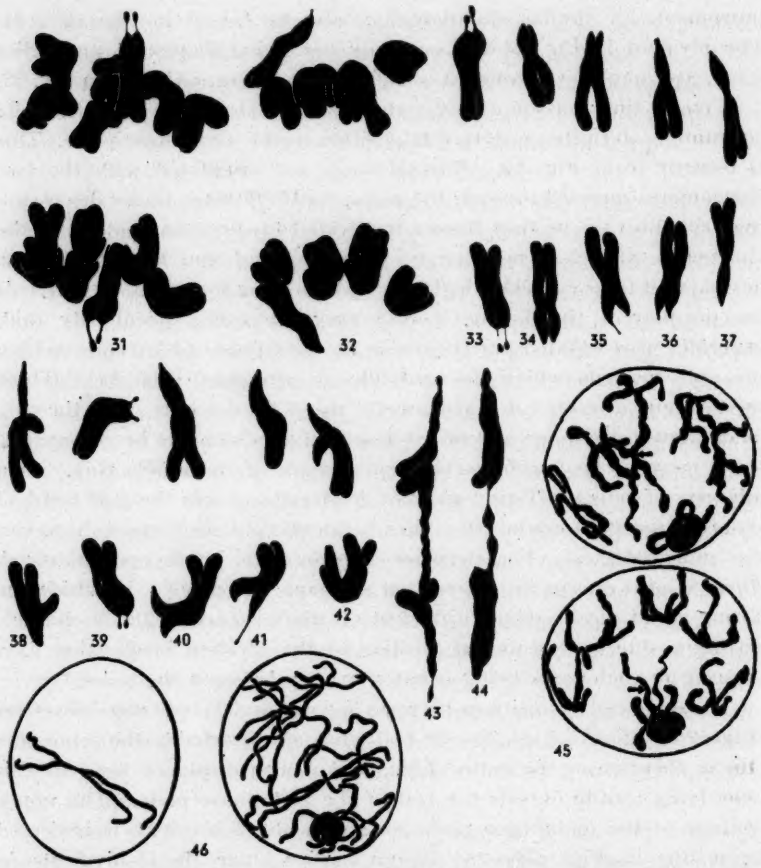
movement. A similar situation may also be traced in Figs. 23—24. The bivalent in Fig. 24 has certainly been ring-shaped at an earlier stage. Its anaphase movement is slightly more advanced than in Fig. 22.

The T-rings have not only a characteristic shape but also a definite orientation and often a deviating position in the metaphase plate. This is evident from Fig. 12. Normal rings are orientated with the two centromeres directed towards the poles. In the T-rings under discussion the »satellite» on its thin thread is directed towards one pole, and the short arm, stretched between the satellited end and the centromere, lies parallel to or coincides with a line connecting the poles. As regards the position of the T-ring, it is a very interesting peculiarity that, generally, it is situated partly outside the metaphase plate, approaching the pole towards which the »satellite» is stretched (Fig. 12). Thus, the terminal attraction towards one of the poles not only gives the ring its characteristic shape and orientation, but also seems to be responsible for a more or less pronounced displacement of the whole ring. In a minority of cells the T-ring was not displaced towards the pole but had a normal position among the other bivalents. In such cases, however, the morphological characteristics appeared to be less pronounced. There is also reason to believe that in many I-M groups, in which the T-ring could not be distinguished at all, the absence of the T-characteristics is due to the normal position of the bivalent in question, i. e. the ring in such cases being situated exactly between the poles.

In some cells transitions between T-rings and T-rods were observed (Figs. 25—30). In Figs. 25—28 both ends are directed to the same pole and in these cases the entire T-bivalent is also displaced towards this pole, lying a little outside the rest of the metaphase plate. The upper contour of the metaphase plate, excepting the T-bivalent, is indicated by a line in Figs. 25—28. At an earlier stage the T-bivalents in Figs. 29—30 have probably been similar to those in Figs. 25—28, but now the short arm of one of the chromosomes has changed direction and points to the opposite pole. In Figs. 29—30 the T-bivalent is situated among the other bivalents, their contours being indicated by a double line.

2. FIRST ANAPHASE.

At first anaphase the T-chromosomes generally have a very characteristic appearance and may usually be distinguished from the other chromosomes at first sight. Such is the case in Figs. 31—32, showing all the chromosomes in two cells at this stage. The T-chro-



Figs. 31—44. First anaphase in plants having a T-chromosome pair. Figs. 31—32, complete groups, the »satellites» or T-ends point to the pole; Figs. 33—37, separate T-pairs, all four chromatids of the short arms pointing to the poles. The T-pairs in Figs. 31—37 are partly derived from rod bivalents, partly from rings. Figs. 38—42, separate T-pairs, all four T-ends not yet pointing to the poles; these chromosome pairs are all derived from ring bivalents. Figs. 43—44, T-bivalents with difficulties of separation, in Fig. 43 in the short (T-)arm, in Fig. 44 in the long arm. (The anaphase figures 31—44 were taken from the following lines and F_1 generations: line 129: Figs. 31, 33, 39; line 128: Fig. 43; line 175: Fig. 44; 128 × 129: Fig. 37; 129 × 175: Figs. 34, 36; 129 × 143 or reciprocally: Figs. 32, 35, 38, 40, 42; 143 × 128: Fig. 41.) Figs. 45—46, interphase, the T-chromosomes stretched through the nuclei; note their submedian centromere separating a long and a short arm; the T-chromosome is not identical with the S.A.T.-chromosome. In the nucleus to the left in Fig. 46 only the T-chromosome is represented, the T-chromosome in the other nucleus having a corresponding position. In Fig. 45 the T-chromosomes are indicated with arrows. (Fig. 45 from 128 × 129; 46 from 129 × 175.) — × 3100.

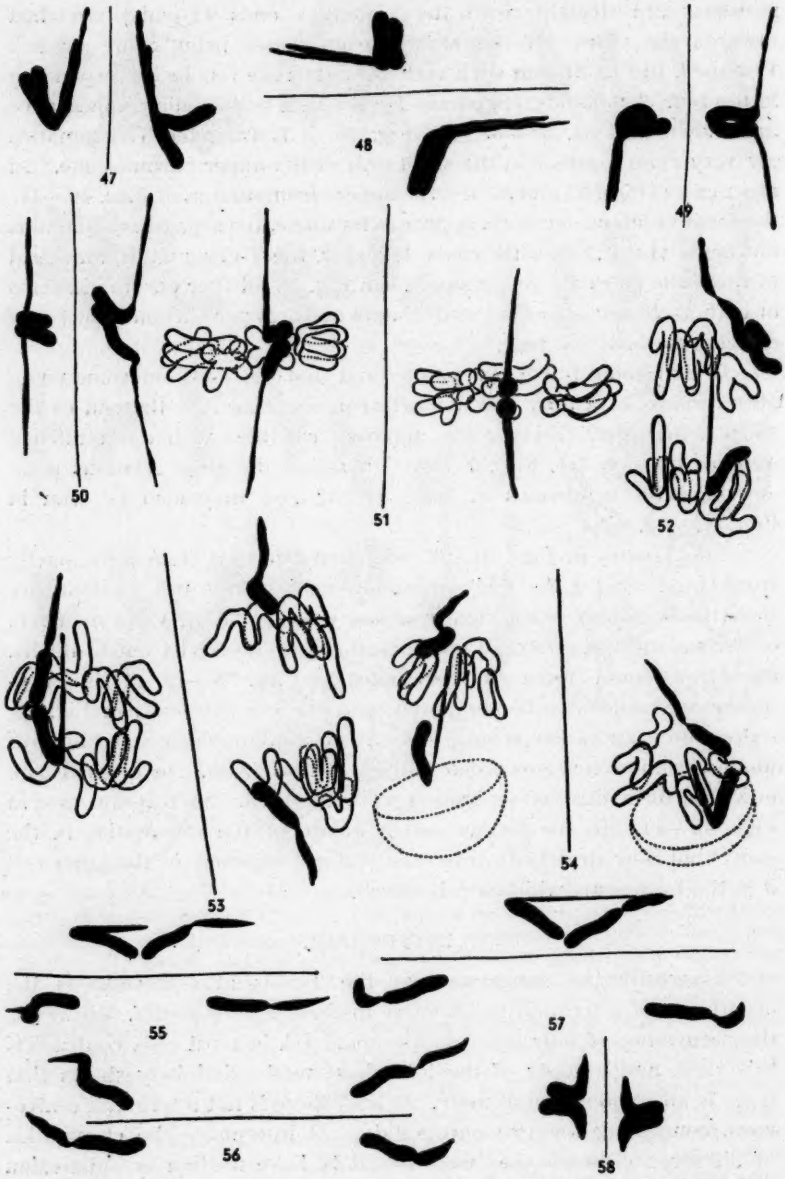
mosomes are straight, with the »satellite» ends (T-ends) stretched towards the poles, all the other chromosomes being more or less V-shaped. In Fig. 31 four such »satellite» ends are visible, corresponding to the four chromatids. Separate T-pairs of a quite similar appearance are shown in Figs. 33—36. In Fig. 36, it is true, the T-chromatids are very close together in the short arm of the upper chromosome. In other cases (Figs. 32 and 37 and the upper chromosomes of Figs. 40—41) the same chromosome parts appear to be single, the separate chromatids not being visible. In some cases, however, the T-chromatids, stretched towards the poles are really single. In Fig. 38 all four chromatid arms of both T-chromosomes are visible, only one arm per chromosome being directed towards the pole.

In describing I-M it was pointed out that the T-chromosome probably consists of a long and a short arm, and that it is the end of the short arm (often carrying the apparent satellite) which is stretched towards the pole (cf. Figs. 7—8). I-A shows the same relations more clearly. This is obvious in Figs. 34—37 and may also be seen in Figs. 38—42.

The T-pairs in Figs. 31—37 are partly derived from rods, partly from rings. At I-A the T-chromosomes coming from rod bivalents are from the beginning in the right position, whereas the previous members of T-rings must be stretched und turned round (especially one of them). Such transitional stages are represented by Figs. 38—42. These chromosomes should also be compared with the chromosomes in Fig. 24, representing an earlier stage. — As a rule the anaphase separation of the T-chromosomes proceeded without disturbances. In a few cases, however, difficulties of separation were observed. Such is the case in Figs. 43—44. In the former cell it is two of the chromatids in the short (but now stretched) arms that will not separate, in the latter cell it is the long arms which are involved.

3. INTERPHASE.

Especially the appearance of the T-rods at I-M suggests the occurrence of a terminal centromere in these chromosomes. However, the occurrence of four separate T-ends at I-A in most cells contradicts this view, and a study of the interphase nuclei definitely shows that there is no terminal centromere. At least there is not a terminal centromere connecting the two chromatids, At interphase the chromatids of all seven chromosomes were found to have median or submedian connections, showing the positions of the centromeres (Figs. 45—46).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In some of the interphase nuclei the T-chromosomes (indicated with arrows in Fig. 45) could be distinguished with certainty. The four arms of these chromosomes were lying rather flat in the same plane, often being stretched through the whole nuclei (Fig. 46). This also means that the arms on the same side of the centromere were somewhat nearer to each other. In the other chromosomes the arms are quite bent and generally extend at right angles from the centromere. The T-chromosomes were evidently most easily visible in interphase nuclei of cells in which the separation of the T-chromosomes at I-A had been rather late. In cells with early separation of the T-chromosomes these chromosomes were pressed at telophase and interphase against the distal parts of the nuclear membrane. In such cells the »satellite» ends of the T-chromosomes were often bent by the pressure, thus making it difficult to distinguish the T-chromosomes from the other chromosomes. — Finally, it should be observed that at interphase the short and long arms of the T-chromosomes were clearly visible, and that the T-chromosome is not identical with the nucleolus-chromosome, the real satellite chromosome (Figs. 45—46).

4. SECOND METAPHASE AND ANAPHASE.

In typical cases the T-chromosomes have a very striking appearance at II-M and II-A. At the former stage (Figs. 47—51) the »short» arm with the »satellite» end, observed at I-M and I-A, is stretched towards the pole and sometimes drawn out into a thin thread. The »long» arm of the T-chromosomes, on the contrary, appears rather short and thick. The centromere is situated at the transition between the thin and thick part of the chromatids. The two »short» arms belonging to the same chromosome are sometimes stretched to the same

Figs. 47—58. Second meiotic division in plants having a pair of T-chromosomes. Excepting Fig. 58, all figures were taken from plants with a high or rather high intensity of the T-phenomena. In order to save space the true distance between the chromosomes and the cell wall (indicated with a line) has been reduced in most figures. Figs. 47—50, the various possible II-M configurations with regard to the orientation of the four T-arms; all figures drawn from the same plant of line 129, just as Fig. 51, which represents a complete II-M. Figs. 52—54, II-A groups, derived from II-M configurations as follows: Fig. 52 (one cell) from e. g. Fig. 47; 53 from 49, 54 from 47; Figs. 55—57, separate T-pairs at II-A, derived from II-M configurations as follows: Fig. 55 from Fig. 47 (the T-arm of the lower chromosome to the left just turning round), 56 from 49 (the T-arm of the upper chromosome to the left just turning round), 57 probably from 49; Fig. 58, T-chromosomes at II-M in a plant of medium intensity. (Figs. 47—58 were taken from the following lines and F_1 generations: line 129: Figs. 47—51, 53, 55, 57; 129 × 175 or reciprocally: Figs. 52, 54, 56; line 128: Fig. 58.) — × 3100.

pole (Figs. 47—48 and Fig. 49, to the left), sometimes to different poles (Fig. 49, to the right, Figs. 50—51). Further, the orientations of the chromatid parts in question are evidently independent of each other in the two metaphase groups of the same p. m. c. Hence the different combinations represented by Figs. 47—50 are realized. In Fig. 51 the entire II-M groups are drawn in natural position. In the other figures the T-chromosomes are separately drawn (more closely together than in their natural position), the black vertical line indicating the cell wall separating the corresponding II-M groups. In some of the T-chromosomes drawn the chromatids are still held together by the centromere, in others the anaphase movement has just started, the chromatids being separated from each other.

The different orientation of the T-chromatids at II-M results in different configurations at II-A. This is well illustrated by Fig. 53, showing the total chromosome complement of a p. m. c. at II-A. In the group to the left the »short» arms of the T-chromosomes are stretched towards the same pole, in the group to the right to opposite poles. At II-M this p. m. c. must have had the arrangement of the »short» arms represented by Fig. 49. The only difference is that the two parallel thin arms to the left in Fig. 49 are bent downwards instead of upwards. Fig. 54 represents another II-A configuration. The position of the T-chromosomes shows that the II-M arrangement in this case must have been of the same kind as in Fig. 47. In the single II-A group represented by Fig. 52 the »satellite» ends of the T-chromosomes are also orientated towards the same pole. In the lower of these chromosomes the »short» arm is drawn out into a very long and thin thread. The same phenomenon may be seen in Figs. 53 and 54. Evidently this chromosome arm is subject to a very marked tension. The anaphase movement pulls the chromosome towards the lower pole, the end of the »short» arm still being attracted to the upper pole. By this apparent attraction to the upper pole the T-chromosome in question only unwillingly moves downwards and is therefore generally lagging somewhat behind the other chromosomes in the same group.

However, when the anaphase movement has proceeded far enough, the influence of the opposite pole seems to lapse. As far as our observations go, the T-end now comes under the influence of the pole to which the anaphase group is moving, and this causes the end to turn round and be stretched in the other direction. This reversal of direction is rather clearly demonstrated by Fig. 55 (the lower chromosome to the left) and also by Fig. 56 (the upper chromosome to the

left). — Before leaving Figs. 47—57, it should be observed that the »short» arm of the T-chromosomes is, on an average, more stretched at metaphase and commencing anaphase than at later anaphase stages. Apparently, the tension to which the chromosome arm in question is subject, is strongest at the first mentioned stages and is diminished more and more as the chromosomes approach the poles. Finally, when the T-chromosome has reached the pole, the short arm is quite contracted and will be bent towards the other arm. This is best shown by Fig. 57 (the lower chromosomes). In the other anaphase of the same p. m. c. the T-chromosomes are just separating.

III. THE OCCURRENCE OF T-CHROMOSOMES IN DIFFERENT INBRED LINES.

1. HOMOGENEOUS LINES.

Most of the material examined was fixed in 1940, but additional data were gathered from fixations made in 1939 and 1941. — During the meiotic studies it was soon realized that the peculiar T-chromosomes occurred in some inbred lines but not in others. Further, it was observed that the characteristic features of the T-chromosomes were expressed to different degrees in different lines. Attempts were made to classify the different lines according to the intensity with which the T-peculiarities were shown. This work was hampered by the following difficulties: (1) The fixation and staining influence the visibility of the phenomenon in question. In slides representing good fixation and not too heavy staining it is easier to detect and study the T-chromosomes than in other less successful slides. (2) The T-chromosomes are easier to detect as rod bivalents than as ring bivalents. This is a source of error, as the relative frequency of rods and rings is different in different lines and F_1 combinations. (3) The various meiotic stages are not equally responsive to differences in the intensity of the T-phenomenon. With decreasing intensity, the T-characteristics disappear earlier at metaphase (I and II) than at anaphase. Unfortunately, in many plants not all four stages were available. (4) The intensity of the phenomena shown by the T-chromosomes is probably also influenced by environmental conditions.

In spite of these difficulties it was possible to refer the material studied to the following categories.

A. HIGH INTENSITY.

At the highest intensity of the phenomenon under consideration the T-chromosomes may be distinguished easily at every stage from I-M to II-A as shown by most of the Figs. 1—57. At I-M typical T-rods as well as T-rings are always visible, their total frequency ranging from 10 to 35 per 50 cells. Thus, the T-chromosomes are not visible in every cell but are distinguished at first glance in a section containing several p. m. c. The very small »satellites» on thin threads (Figs. 1—3) are characteristic of this high intensity. At I-A the pairs of corresponding elongated T-chromosomes are clearly seen in most cells, and this is also true of II-M, showing the typical thread-like, outstretched chromosome arms. At II-A the T-chromosomes are often visible in all four anaphase groups. At this stage the long thin threads present in some cells are especially striking. As explained above, they arise when the terminal end is directed towards one pole and the submedian centromere moves towards the opposite pole (cf. Figs. 52—54). This group is represented by a single line, No. *129*. The typical mode of meiosis described in Chapter II is primarily based on the conditions in this line.

In 1940 two plants of line 129 were studied, and in both plants all the four main stages (I-M, I-A, II-M and II-A) wer available. In both plants 50 cells at I-M were analysed. In the first plant, 129—1, 22 of the I-M groups had T-rod bivalents, 11 had T-rings and 17 no clearly visible T-bivalents. The average frequency of rod bivalents was 1,26 per cell. In the other plant, 129—13, the corresponding figures were 16 T-rods, 8 T-rings and 26 I-M groups without visible T-chromosomes. Rod bivalent frequency: 0,96 per cell. — In 1941 five plants of line 129 were studied, and in four of them I-M stages were available. Without exception these I-M stages revealed the presence of T-rods as well as T-rings, though in a somewhat lower frequency than in the preceding year. I-A occurred in three of the plants, and quite typical T-chromosomes were observed in most cells at this stage. II-M and II-A could also be observed in three plants. The striking appearance of the T-chromosomes at these stages was somewhat less pronounced than in the plants fixed in 1940.

B. MEDIUM INTENSITY.

In this category there is a lower frequency of visible T-rod bivalents at I-M than in Group A. Moreover, those which can be distinguished are less typical. They are less elongated and the »satellite» is less pronounced or may even be quite absent. Compare Figs. 1—3 (high intensity) with 4—6 (medium intensity). Therefore, the T-rod bivalents may sometimes be difficult to distinguish from ordinary rod bivalents. T-rings are quite rare or may be entirely missing. At I-A the T-chromosomes are quite or almost as clearly seen as in Group A. The II-M

stage is highly variable even in the same slide. Some pairs of cells do not show any T-chromosomes at all, in other p. m. c. there are from one to four rather weakly accentuated points (cf. Fig. 58), whereas in a few cells the T-chromosomes may be as clearly visible as in Group A. At II-A the T-phenomenon is almost as regularly and clearly visible as in Group A, but the thread-like, very much stretched, »short» arms (cf. Fig. 52) do not occur in Group B. This group is represented by line *175*.

Two plants of line 175 were studied in 1940 and two in 1941. In three of these plants there were less than ten T-rod bivalents per 50 cells, and only in one of these three was a single T-ring observed. In the fourth plant the occurrence of T-chromosomes appeared to be almost as pronounced as in line 129 (Group A), ten T-rod bivalents and six T-rings being observed per 50 cells. Some of the T-rod bivalents were even as typical as the one represented by Fig. 1. It is not known whether this deviating behaviour indicates a genotypical heterogeneity of line 175, or whether the stronger T-tendency in the last mentioned plant is only due to environmental conditions. On an average, however, the frequency of T-chromosomes at I-M was lower in line 175 than in line 129. This is not correlated with a lower total frequency of rod bivalents in line 175, which would tend to reduce the chances of detecting T-bivalents. On the contrary, the four plants examined had on an average 1,64; 1,68; 1,68 and 1,73 rod bivalents per cell, the corresponding values of five plants of line 129 being 0,61; 0,80; 0,84; 0,96 and 1,26 respectively. — I-A could be studied in three of the plants, II-M and II-A only in one plant.

C. LOW INTENSITY.

In this group no T-bivalents, whether rods or rings, are visible at I-M. At I-A, however, the T-chromosomes are visible in one half to one third of the cells, but they are not as typical as the T-chromosomes illustrated by Figs. 31—37. Often the T-ends of all four chromatids are directed towards the poles, it is true, but the chromosomes are less elongated. The II-M stage does not show any T-chromosomes at all. The same is true of many cells at II-A, but in other cells there are from one to four points, corresponding to the T-ends of the T-chromosomes. This category is represented by line *143*.

The weak T-phenomena in line 143 were at first entirely overlooked. However, in connection with the study of the F_1 combinations in 1941 we had to re-examine the slides of the parent lines also, and during this work the indubitable T-characteristics of line 143 were discovered. At I-M the frequency of rod bivalents in line 143 seems to be even higher than in line 175, the average values of three plants examined being 2,33; 0,98 and 2,48. In spite of this only one single possible T-rod bivalent and perhaps one single T-ring could be distinguished in all three plants. — The first division was studied in three plants, the second in only one of them.

D. TRACES OF T-CHROMOSOMES?

In this category traces of T-chromosomes were seen a few times at I-A and II-A (one or two points) and possibly also at I-M. At II-M T-chromosomes were never observed. In this group the lines *173*, *185*, *131* and *133* may be included.

Three plants of line 173 were examined. One of these (from 1940) had only second division stages and showed no T-ends. Two plants fixed in 1941 contained all stages from I-M to II-A. In both plants single cells at I-M contained possible T-rod bivalents with one or both the free ends pointing towards the poles. Also in a few cells at I-A a pair of chromosomes was observed with one to three points more or less clearly directed towards the poles. In one of the plants weakly pronounced points were a few times observed on *two* pairs of chromosomes. In this group it was not possible to decide whether the apparent T-phenomena are really displayed by a special chromosome pair, and whether this pair corresponds to the T-chromosomes observed in the previous groups (A—C). — Similar weak evidence of T-points orientated towards the poles was obtained in one or a few plants of lines 185, 131 and 133.

E. NO T-CHROMOSOMES.

In most of the inbred lines T-chromosomes were completely absent at all stages from I-M to II-A. This is true of 24 lines, a total of 63 plants being examined. It should be pointed out that the groups D and E are not clearly separated. On the other hand, these groups differ sharply from the groups A, B and C. The latter groups give the impression of being »homozygous for a terminal centromere». As already pointed out, however, this is not the true explanation of the peculiar meiotic behaviour of these lines.

2. A HETEROGENEOUS LINE.

The line *128* was studied for three years and was found to be heterogeneous as regards the occurrence of T-chromosomes and the degrees of their manifestation. This heterogeneity was also verified by a study of the F_1 hybrids obtained in crosses between 128 and other lines (cf. below).

In line 128 a total of seven plants were examined and were found to represent most of the intensity groups A—E discussed above. In one plant only I-M was available, but as many typical T-rods and also some T-rings were present, it may be considered to have an intensity intermediate between those of groups A and B. In four other plants, in which all four main stages were available, the intensity of the T-phenomenon was less marked. Two plants were considered to fall into the

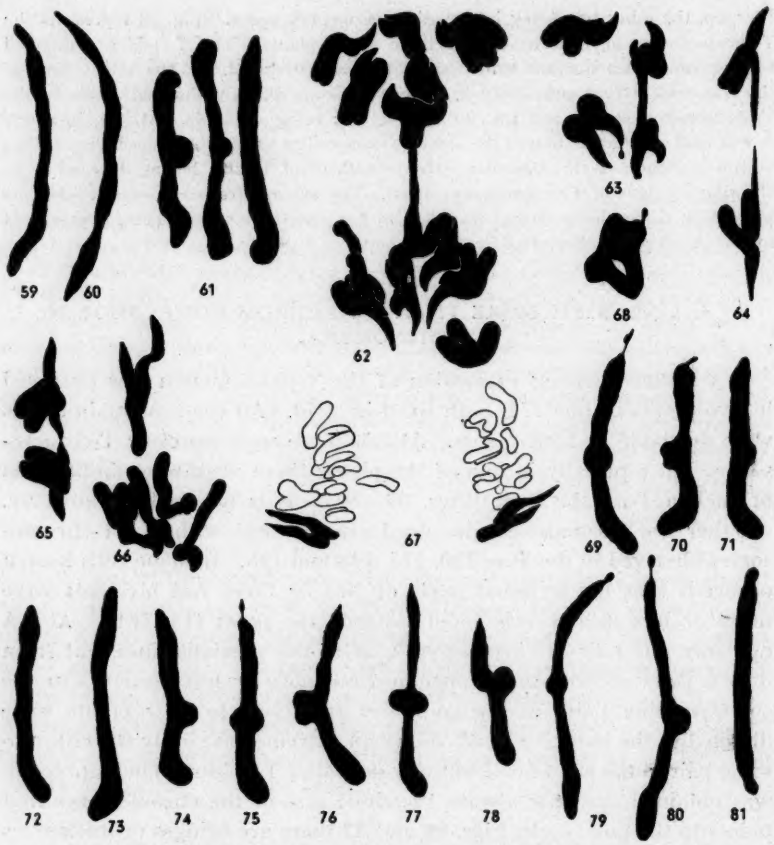
B-group, the other two being intermediate between B and C. Fig. 58 represents the T-chromosomes at II-M in one of these latter plants. The T-ends are directed towards the poles but are rather short and not stretched. — The sixth plant of line 128 was at first considered to belong to Group D, only showing traces of the T-phenomenon at I-M and I-A, no other stages being available. At last, however, it was realized that it showed the same characteristics as the F_1 plants between lines with and without T-chromosomes. The seventh plant, finally, belonged to Group E, showing no signs of T-chromosomes at all. The average frequency of rod bivalents per cell in these plants ranged from 1,58 to 2,70, the former value being represented by the A—B-plant, the latter by the E-plant.

3. A LINE WITH MORE THAN TWO CHROMOSOMES SHOWING T-PHENOMENA.

A rather puzzling expression of the T-phenomenon was observed in two plants of line *171*, both fixed in 1940. All the four main stages were available in both plants. At I-M there were no clear T-chromosomes, but especially in one of the plants there were some indications of such a T-rod bivalent (Figs. 59—60). It is not certain, however, whether the chromosomes involved are identical with the T-chromosomes observed in the lines 129, 175, 143 and 128. In some cells it even occurred that the terminal parts of two or three rod bivalents were more or less clearly orientated towards the poles (Fig. 61). At I-A not only one pair of chromosomes, as in the previous lines, but from 0 to 6 pairs showed the T-phenomenon more or less clearly. In the corresponding pairs of chromosomes from one to four points were directed to the poles. Fig. 62 shows an extreme case, only the chromosome pair to the right being entirely devoid of T-points. The impression was obtained that it is always the short arm of the chromosomes that points to the pole. — In Figs. 62 and 63 there are bridges or difficulties of separation in the chromatids without terminal tendency, in Figs. 64 and 65 there are difficulties of separation between the chromatids with terminal tendency.

At II-M the chromosomes only rarely showed a weak T-tendency. At II-A many groups were regular, without T-phenomena. In some cases, however, a single rather clear T-chromosome was observed and, finally, it happened not infrequently that from one to five arms in an anaphase group showed a tendency to polar orientation or transitions from non-polar to polar direction (Fig. 66).

In line *136* and possibly also in some other lines (cf. line 173. p. 454) a tendency to T-behaviour in more than one chromosome pair was also noticed, but this tendency was much weaker than in line 171.



Figs. 59—66. Chromosomes from line 171, showing a weak T-tendency in a variable number of its chromosomes; Figs. 59—60, I-M rods (rarely found; not more than one per cell) resembling the T-chromosomes in the lines 129 or 175; Fig. 61, three rod bivalents at I-M from the same cell, all three with a very weak T-tendency; Figs. 62—65, first anaphase; Fig. 62, a complete I-A, representing the most extreme case of T-tendency among the cells studied. Fig. 63, two chromosome pairs with a clear T-tendency. Figs. 62 and 63 show a bridge or difficulty of separation between chromatids without T-tendency. Figs. 64—65, difficulties of separation between chromatids with T-tendency; Fig. 66, T-tendency in II-A chromosomes (the group incomplete). Fig. 67, I-A in a cell with premature centromere division from an F_1 plant of the cross 175 (medium) $\times$ 143 (low intensity). T-chromatids black, the other chromatids in outline. Figs. 68—81, I-M bivalents from F_1 plants of crosses between lines with and without T-chromosomes. Fig. 68, the only structure which possibly represents a heteromorphic T-ring bivalent, all other rings being apparently normal; Figs. 69—78, more or less clearly heteromorphic T-rod bivalents; Figs. 69—70 (from 129 $\times$ 185) with a clear T-tendency in the upper chromosome; Figs. 71—74

IV. THE OCCURRENCE OF T-CHROMOSOMES IN F_1 HYBRIDS BETWEEN INBRED LINES.

In 1940 eight different inbred lines were selected for crosses. As these crosses were also undertaken with a practical purpose in mind, care was taken to select unrelated vigorous lines that also appeared to be morphologically uniform. Five of the lines selected are derived from five different population plants. The remaining three lines (173, 175 and 180) descend from a sixth population plant. All the lines used for the crosses had been inbred for about 15 years. When the lines were selected, nothing was known about their cytology. Afterwards we were surprised to find that the four lines clearly showing the T-phenomenon (129, 175, 143 and 128) were all among the lines selected for the crosses. This is probably not a mere chance occurrence, as is evident from the following figures. Of the 34 lines cytologically studied eight were used for crosses, 26 not used. In the former category the proportion of lines with and without T-chromosomes was 4 : 4, in the latter category 26 : 0. These values cannot represent the same distribution. A statistical test by the most accurate method available (cf. BONNIER and TEDIN, 1940, pp. 226—228), gives a P-value of only 0,0015. The reason of this difference in distribution is rather obscure, the only differences between the lines used for the crosses and those not used being a higher average degree of vigour and uniformity in the former category.

The lines used for the crosses and their properties as regards the T-phenomenon were as follows: 129 (Group A, high intensity), 175 (Group B, medium intensity), 143 (Group C, low intensity), 128 (heterogeneous), 173 and 185 (Group D, traces of T-chromosomes?), 138 and 180 (Group E, no T-chromosomes). The best survey of the behaviour of the T-chromosomes in the hybrids produced will be obtained by arranging the crosses in the following four groups:

1. Crosses between members of Groups A—C, both parent lines showing the T-phenomenon.
2. Crosses between members of Groups D and E, the parent lines without T-chromosomes or with possible traces of T-chromosomes.

(from 175 × 173 and 175 × 180) with a very weak T-tendency; Figs. 75—78 (from 128 × 185) with a clear or rather clear T-tendency. In Figs. 79 (175 × 185) and 80 (128 × 185) the lower short arm is also polar-directed, but without clear T-characteristics. Fig. 81 (175 × 173) probably represents the S.A.T.-chromosome pair, not the T-chromosomes. — Fig. 67, × 2100. The other figures × 3100.

3. Crosses between members of Groups A—C (occurrence of T-chromosomes) on one side and members of Groups D—E (no T-chromosomes or possible traces) on the other side.
4. Crosses involving the heterogeneous line 128.

Of these cross-categories, numbers 1 and 3 are of most interest and will be considered in detail.

1. BOTH PARENTS WITH A T-CHROMOSOME PAIR.

A. THE CROSS 129 (HIGH INTENSITY) × 175 (MEDIUM INTENSITY) AND RECIPROCALLY.

In this F_1 combination three plants from the cross 129 × 175 and three plants from 175 × 129 were examined. In all these plants the T-phenomena were clearly visible. Two plants (one from each reciprocal cross) were classified as having high intensity like the parent line 129, the other four F_1 individuals were considered to be intermediate between »high» and »medium» intensity. In the F_1 plants the T-phenomena at the first division were, on an average, almost as pronounced as in line 129, but at the second division they were somewhat less striking. Thus, considering all data, the T-phenomena in the F_1 plants were intermediate between the parents, but with a rather marked prevalence for the high-intensity parent line, 129.

A few detailed values may be mentioned. In four F_1 plants the number of T-rod bivalents and T-rings per 50 cells was counted. In the first plant there were two rods and five rings, in the second one rod and eight rings, in the third one rod and six rings and in the fourth four rods and 34 rings (the second division of this latter plant was, unfortunately, not available). Thus in F_1 there is a higher proportion of T-rings than T-rods in contrast to the parent line 129, in which the T-rods were more frequent. This is connected with the general fact that the chiasma frequency in F_1 hybrids between inbred lines of rye is higher than in the parent lines (PRAKKEN and MÜNTZING, unpublished data). Thus, in the F_1 hybrid now under discussion the general frequency of rod bivalents was rather low, the values of five plants ranging from 0,24 to 0,64. In the parent lines the average values were 1,11 (line 129) and 1,69 (line 175). Under such circumstances the chances of observing T-rod bivalents at I-M in the F_1 must be rather small, practically all bivalents being ring-shaped. In good slides, however, the T-chromosomes may also be recognized as rings. The slide showing as many as 34 T-rings per 50 cells is an extreme example of this kind.

B. THE CROSS 129 (HIGH INTENSITY) × 143 (LOW INTENSITY) AND RECIPROCALLY.

In this F_1 combination two plants from the cross 129 × 143 and three plants from 143 × 129 were examined. The main result of this

examination was that, on an average, the F_1 plants were intermediate between the parents as regards the T-phenomena, though with a good deal of variation between plants, slides and stages. Taking all data together, it was also obvious that in the present F_1 hybrids between »high» and »low» intensity the T-phenomena were somewhat less marked than in the F_1 hybrids between »high» and »medium» intensity.

A few frequency values may be mentioned. At I-M the frequency of T-rod bivalents and T-rings per 50 cells in five plants examined was found to be $1 + 7$, $1 + 0$, $4 + 27$, $1 + 8$ and $2 + 0$ respectively, the first value in each pair indicating rod bivalents, the second value ring bivalents. According to these values, the frequency of T-bivalents is highly variable, ranging from 1 to 31 per 50 cells. In reality the variation is probably not as strong as indicated by the figures. In some slides the T-chromosomes may have been difficult to detect, if the staining had been too heavy. T-chromosomes are also easier to detect at late I-M than at early I-M. In this F_1 combination, too, T-rings were relatively more numerous than T-rods. This is again connected with the fact that the frequency of rod bivalents was much lower in the F_1 plants than in the parent lines. In the F_1 plants the number of rod bivalents per cell ranged from 0,34 to 0,70, in the parent lines the average values were 1,11 (line 129) and 1,66 (line 143).

In this F_1 combination, as well as in the preceding one, our attention was directed to the possible occurrence of heteromorphic T-bivalents. The occurrence of such bivalents and pairs of chromosomes at later stages might be expected, as the appearance of the T-chromosomes in the »high-intensity» line 129 is rather different from the appearance in the »medium» and »low» lines 175 and 143. However, no clear evidence of this kind could be gathered. On the contrary, in several cases the T-arms of the corresponding chromosomes were found to be quite equal in appearance at I-M, with both ends decidedly more pronounced than is ever the case in line 143. At I-A and later stages it was also observed that the four T-ends, corresponding to the four chromatids constituting the T-bivalent, were often equally well developed. Especially at II-M they showed an intensity never occurring in line 143. Thus, the F_1 plants of the crosses 129×175 as well as 129×143 appear to be »homozygous» for the T-chromosome. However, as already pointed out, the degree of expression of the T-phenomena is different in the two crosses, being somewhat more pronounced in 129×175 than in 129×143, but in both F_1 combinations less marked than in the »high-intensity» parent line 129.

C. THE CROSS 175 (MEDIUM INTENSITY) $\times$ 143 (LOW INTENSITY).

In this hybrid combination three plants from the cross 175×143 were examined. At I-M practically no T-chromosomes could be detected,

only a few doubtful cases being recorded. At I-A, on the contrary, the T-chromosomes could be seen almost regularly in one slide and in about half of the cells in a slide from another F_1 plant. The peculiarities of the T-chromosomes were not very marked, but in several cases all four T-arms were visible and directed towards the poles. An exceptional I-A cell, in which the centromeres of all chromosomes had undergone a premature division, is represented by Fig. 67. In this cell the four chromatids of the T-pair are also separate and strikingly different from the other chromatids. At II-M no evidence of T-chromosomes could be detected, and at II-A they were rather rare. In some p. m. c., however, one to three weak T-points could be distinguished at II-A.

In general it can be stated that this F_1 combination also is »homozygous» for the T-chromosome. The intensity is intermediate between the parents but apparently with a rather pronounced prevalence for the parent, 143, of lowest intensity.

2. BOTH PARENTS WITHOUT CLEAR T-CHROMOSOMES.

This category is only represented by one cross combination, viz. 173 × 180 and reciprocally. Line 180 does not show any T-chromosomes at all, and in line 173 only possible traces of such chromosomes were observed. Five F_1 plants were examined, I-M and I-A stages being available in all of them, II-M and II-A in two plants. As might be expected, no signs of T-chromosomes were detected in any of the plants.

3. CROSSES BETWEEN PARENTS WITH AND WITHOUT A T-CHROMOSOME PAIR.

In this category, involving six different F_1 combinations, the parents with T-chromosomes belong to the groups A, B and C, showing different intensities of the T-phenomenon. The parents without T-chromosomes, or with possible traces only, belong to the groups D and E. Thus, the F_1 plants are heterozygous as regards the T-chromosomes. This heterozygosity is important, as it offers possibilities of deciding whether the T-phenomena are gene-controlled, due to structural chromosome differences, or to an interaction of both these factors.

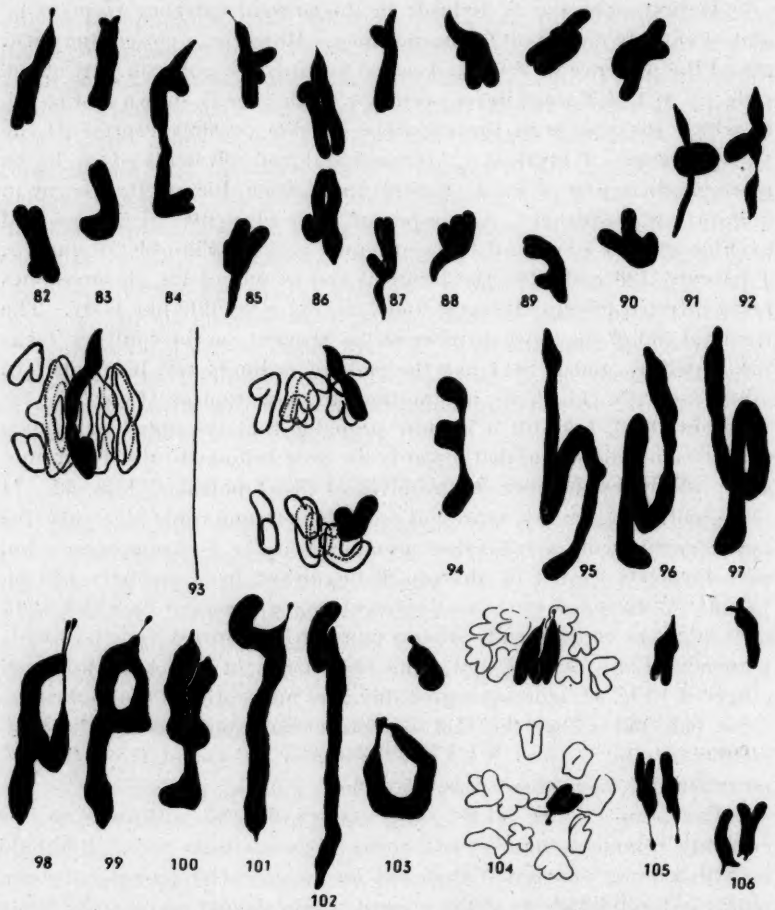
In the six F_1 combinations meiosis was studied in a total of 22 plants. I-M stages were available in all these plants, I-A in 19 plants, II-M and II-A in 15 plants. The behaviour of the T-chromosomes was essentially similar in the six different F_1 combinations, and hence a general account of the observations may first be given, followed by some special data characterizing the different F_1 hybrids.

At first sight the F_1 hybrids in the present category seem to be almost entirely devoid of T-chromosomes. However, a closer study will reveal the presence of T-ends, directed towards the poles, in part of the cells. — At I-M T-rings never occur. A single case is shown in Fig. 68, in which the ring with the apparent satellite possibly represents the »heterozygous» T-bivalent. Asymmetrical rod bivalents seem to be more characteristic of the F_1 hybrids in question, though they occur in quite a low frequency. A number of such bivalents are represented by Figs. 69—78. Some of them are quite typical (Figs. 69, 70 and 75; T-parents: 129 and 128), the terminal end of one of the chromosomes being directed towards the pole and carrying a satellite-like body. The terminal end of the other member of the bivalent, on the contrary, lacks the »satellite» and is bent like the ends of ordinary rod bivalents. In other cases the bivalents in question are less typical (Figs. 76—78; T-parent: 128), but still it is quite probable that the upper acuminate chromosome end orientated towards the pole belongs to the T-chromosome, the other member of the bivalent being normal. Figs. 71—74 (T-parent: 175), finally, represent possible heteromorphic bivalents (the upper member of each bivalent possibly being a T-chromosome), but such bivalents cannot be sharply distinguished from ordinary rod bivalents. — In a few cases rod bivalents were observed in which both ends might be considered to show a more or less pronounced »terminal» tendency (Figs. 79—81), but quite clear cases of this kind were not observed. Fig. 81, moreover, probably does not represent the T-chromosome pair but rather the real satellite chromosome pair. The non-identity of the T- and S.A.T.-chromosomes is evident from the observations of interphase (Figs. 45—46).

Excepting Fig. 81, all the other figures, 69—80, with more or less certainty represent the »heterozygous» T-chromosome pair. It should be pointed out, however, that the frequency of apparently heteromorphic T-rod bivalents in the present cross-category seems to be lower than the frequency of »homozygous» T-rod bivalents in cross-category 1, in which both the parents have T-chromosomes.

The appearance of T-chromosomes at I-A in the present category of F_1 hybrids is shown by Figs. 82—90. Structures of this kind occur in varying numbers in different F_1 combinations, the ratio of cells with visible T-chromosomes ranging from $^1/_{10}$ to $^2/_3$ approximately.

In Figs. 82 and 83 one member of the corresponding anaphase chromosomes is of ordinary appearance without T-ends. In the other member of the pair both ends of the short arm are evidently directed



Figs. 82—93. Meiosis in F_1 plants of crosses between lines with and without T-chromosomes (continued). Figs. 82—90, first anaphase. Figs. 82—83, the upper chromosome with two T-arms, the lower one normal without T-arms; Fig. 84, only one chromatid shows the T-character; Figs. 85—88, each chromosome with one T-arm and one normal arm; Figs. 89—90, very weakly pronounced (uncertain) T-arms in a hybrid 185 × 143. (Figs. 82—90 are taken from the following F_1 combinations: 128 × 185: Fig. 82; 175 × 180: Fig. 83; 175 × 173 and reciprocally: Figs. 84, 86; 175 × 185: Fig. 85; 128 × 175: Fig. 87; 185 × 143: Figs. 89—90; Fig. 88 is from a »heterozygous» plant of line 128.) Figs. 91—92, II-M chromosomes with two T-arms (from 129 × 185; the corresponding chromosome in the other cell without T-arms; cf. Figs. 82—83). Fig. 93, II-A, in each cell a T-chromosome and a corresponding normal chromosome (from 129 × 185; cf. Figs. 85—88). Fig. 94, a chromo-

towards the pole. Such pictures are very rare, however, and in almost all cells in which T-chromosomes are visible the situation illustrated by Figs. 84—88 is met with. In some cases only one acuminate chromatid arm with polar orientation may be seen in one of the chromosomes (Fig. 84). In the other, more numerous, cases the short arm of each chromosome has one chromatid with polar orientation and one chromatid which is bent in the usual way (Figs. 85—88). Severe efforts have been made to find anaphase pairs which show three or four and not only two T-ends with polar orientation, but clear cases of this kind have not been observed.

At II-M there are in most hybrids no T-chromosomes to be seen. Only in hybrids involving the »high-intensity» T-line 129 as one parent do T-points occur, but they are much less developed than in line 129 itself. Their number was found to range from 0 to 2 per cell-pair (of the same p. m. c.), no clear cases with three or four points being observed. When two points are present they may either occur in the same cell, representing the ends of the two chromatids of the same chromosome (Figs. 91—92), or there is one point in each cell. The latter case is the normal one, whereas the first only rarely occurs. This is in agreement with the I-A relations described above and also with KATTERMANN's observations (1939).

At II-A part of the p. m. c. do not show any T-chromosomes at all, in other p. m. c. there is a total of one or two T-points. In a few cases both T-points are in the same cell, but usually each cell has one point. Fig. 93 shows the chromosomes in a p. m. c. with one II-A and one commencing II-A. In each cell there is a pair of heteromorphic chromatids, one chromatid in each pair having a T-end, the other being normal. At II-A the T-ends, when visible, are usually rather short and contracted, not being stretched to thin threads as in some of the parent lines with T-chromosomes.

After this general description of meiosis in hybrids between parents with and without T-chromosomes a few special data concerning the different crosses in this category may be given.

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some pair with a typical constriction (from a pure line 138 plant, occurring among F_1 plants of the cross 138 × 143). Figs. 95—97, associations of four chromosomes in an F_1 plant of the cross 180 × 175. The upper chromosome in each quadrivalent probably represents the T-chromosome. Figs. 98—106, the T-chromosomes in a triploid plant of line 129. Figs. 98—102, trivalents of different types at I-M; Fig. 103, bivalent + univalent; Fig. 104, a complete I-A (T-chromosomes in black); Figs. 105—106, separate T-chromosomes at I-A, two passing to one pole, one to the other pole. — Figs. 104—106, × 2100. The other figures × 3100.

A. 129 × 185 AND RECIPROCALLY.

In this F_1 combination between »high intensity» (line 129) and »traces?» (line 185) three plants were examined. At I-M the number of heteromorphic T-rod bivalents is quite low, such structures being estimated to occur in something between 0 and 2 per cent of the p. m. c. (Figs. 69—70). At I-A one or two T-points occurred in respectively 15 and 25 per cent of the cells in slides from two different F_1 plants. In this F_1 combination, in contrast to the other F_1 hybrids of this cross-category, T-points were also visible at II-M (Figs. 91—92). However, they only occurred in part of the cells and had never a pronounced appearance. At II-A many cells showed no T-points, in others there were clearly one or two (Fig. 93). In a few cells even the very characteristic thread-like structure occurring in »high-intensity» lines and F_1 families (cf. Figs. 52—54) could be seen, viz. the thin thread connecting two anaphase groups, this thread representing the »short» arm, which is stretched between the moving centromere and the T-end attracted to the opposite pole.

B. HYBRIDS BETWEEN LINE 175 AND LINES 173, 180 AND 185.

Line 175 shows T-chromosomes with »medium intensity». Of the other lines 180 has no T-chromosomes, 173 and 185 possibly showing traces of such chromosomes. In the F_1 combinations 175 × 173 (and reciprocally), 175 × 185 and 175 × 180 (and reciprocally) a total of 14 plants were examined, which showed essentially the same meiotic conditions. At I-M, observed in 13 plants, the percentage of cells with heteromorphic T-rod bivalents (Figs. 71—74) varied from about 0 to 3. At I-A, studied in 11 plants, one or two T-points were observed in 20 to 65 per cent of the cells. Thus, in these hybrids there seems to be a higher frequency of visible T-chromosomes at the first division than in the hybrid 129 × 185. At II-M, on the contrary, no clear T-points could be found in the six F_1 plants examined. At II-A most cells had no T-chromosomes, but in a few p. m. c. in all seven plants examined there were one or two T-points. Thus, in the second division the T-phenomena are decidedly less pronounced than in 129 × 185.

Two exceptional F_1 plants in the present category differed from the others in the following ways. In the cross 175 × 180 one plant was found to be homozygous for the T-chromosomes, the intensity of the T-phenomena being medium or rather low. The plant is supposed to have arisen by self-fertilization, the cross in this case being unsuccessful. The other deviating plant belonged to the cross 173 × 175. In this plant T-points were observed at I-A in more than one chromosome pair as in line 171 discussed above. It was not possible to distinguish the true T-chromosomes from other chromosomes with a similar behaviour. Two slides of this plant were examined. The T-phenomenon was more pronounced in one of the slides than in the other one. A sister plant from the same cross, 173 × 175, also showed a similar general T-tendency, but this was very weakly expressed.

C. HYBRIDS BETWEEN LINE 143 AND LINES 138 AND 185.

Line 143 shows T-chromosomes with a low intensity, line 138 has no T-chromosomes and in line 185 there are possibly traces of T-chromosomes. In the F_1 combinations 143 × 138 and reciprocally, 143 × 185 and reciprocally, a total of five

plants were examined. These F_1 plants only show very weak traces of T-chromosomes. The stages I-M, II-M and II-A were almost completely devoid of T-points with polar orientation. Only at I-A were one or two weakly pronounced but probable T-points observed in 10 to 15 per cent of the cells. These supposed T-chromosomes cannot be sharply distinguished from ordinary anaphase chromosomes. This is evident from Figs. 89 and 90, showing I-A chromosomes in a hybrid between lines 143 and 185. In brief it may be said that the T-phenomena in the present category are much less pronounced than in the F_1 hybrids involving lines 129 and 175.

A single plant from the cross 138 × 143 was found to be a pure line 138-plant, representing an unsuccessful cross. It showed absolutely no T-chromosomes at any stage. Further, it had the rather high frequency of univalents and rod bivalents at I-M characteristic of line 138 and, finally, it showed in one of the chromosome pairs typical constrictions (Fig. 94) which are known to be present in some inbred lines but hardly ever in F_1 plants.

4. CROSSES INVOLVING THE HETEROGENEOUS LINE 128.

Though morphologically rather uniform the line 128, as reported above (p. 454), was found to be heterogeneous as regards the T-phenomena. This heterogeneity was verified by a study of the F_1 hybrids involving line 128 as one parent. Before going into details, it should be mentioned that for practical reasons the crosses were generally not performed between individual plants, the pollen being collected and mixed from many plants of the same plot. When sowing the hybrid seeds it was also necessary to mix seeds from different mother plants. Thus no segregation ratios as regards the T-phenomena could be obtained.

A. 128 × 129.

From this cross only one single F_1 plant was available, but in this plant all stages of interest could be thoroughly studied. Figs. 7—10, 15, 24, 37, 45, 118 and 119 were taken from this plant. The plant was obviously homozygous as regards the T-chromosomes, though a few rod bivalents were apparently heteromorphic (Fig. 10). The intensity of the T-phenomena in this plant may be described as being intermediate between »high» and» medium», thus representing about the same degree as in the F_1 hybrids 129 × 175 and 129 × 143.

As an example the following detailed observations on meiosis in this plant may be reported. *I-M* was examined in 50 cells. In 27 of these cells there were 7 ring bivalents, in 20 cells 6 rings + 1 rod bivalent and in 3 cells 5 rings + 2 rods, the average number of rods per cell thus being 0,52. In the same cells a total of 11 T-rod bivalents and 6 T-rings were observed. At *I-A* 50 cells were also examined. In 34 of these the T-chromosomes were clearly visible, in 11 cells the identification of T-chromosomes was questionable and in 5 cells they could not be distinguished at all. At *interphase* the T-chromosomes were sometimes clearly visible. The *II-M* stage was found to be highly variable. In the slide from which the I-M and I-A data were gathered II-M could also be observed but generally showed no T-points

or one to three weak points. In another slide of the same plant II-M showed clear T-phenomena, from one to four T-points being visible in most cells. On account of this variability at II-M, and also at other stages, the classification of the T-phenomena into different categories of intensity is obviously rather difficult. — At *II-A* the T-points were rather pronounced. Their number ranged from 1 to 4, all four points often being visible.

B. 128 × 175 AND RECIPROCALLY.

In this F_1 combination eight plants were available for meiotic examination. These F_1 plants were different as regards the T-phenomena, thus demonstrating the heterogeneity of line 128. As reported above (p. 452), line 175 shows the T-phenomena with a medium intensity. Four of the F_1 plants were found to be »homozygous» for the T-chromosome. The intensity of the T-phenomena in these four F_1 plants was intermediate between »medium» and »low». The other four F_1 plants were found to be »heterozygous», i.e. showing the T-phenomena in about the same way as the hybrids between lines 129, 175 and 143 on one side and lines without T-chromosomes on the other side.

C. 128 × 143 AND RECIPROCALLY.

In this cross between the heterogeneous line 128 and line 143, showing the T-phenomena in a low intensity, five F_1 plants were available for examination. One of these plants, however, turned out to be a pure line 128 plant (»heterozygous» for the T-chromosome), judging from the frequency of univalents and rod bivalents at I-M and from the presence of a chromosome with a typical constriction (cf. Fig. 94). As already mentioned, this chromosome occurs in some inbred lines but is seldom seen in F_1 hybrids. The remaining four plants were evidently true F_1 individuals. Three of them could be classified as being »homozygous», showing the T-phenomena with an intensity ranging from »medium» to »low». The fourth plant, finally, was found to be »heterozygous», thus demonstrating once more the heterogeneity of line 128.

D. 128 × 185.

In this cross between the heterogeneous line 128 and line 185, having possible traces of T-chromosomes only, four F_1 plants were examined. Two of these were completely without T-chromosomes, the other two were found to be »heterozygous».

As a summary of the results gathered from the F_1 hybrids involving line 128 as one parent it may be stated that in all crosses with the »homozygous» lines (129, 175 and 143) the result has been »homozygous» and »heterozygous» F_1 plants. In crosses with a line without T-chromosome (185) the result was »heterozygous» plants and plants without T-chromosomes. These data are evidently quite consistent with the fact that line 128 is heterogeneous as regards the T-phenomena.

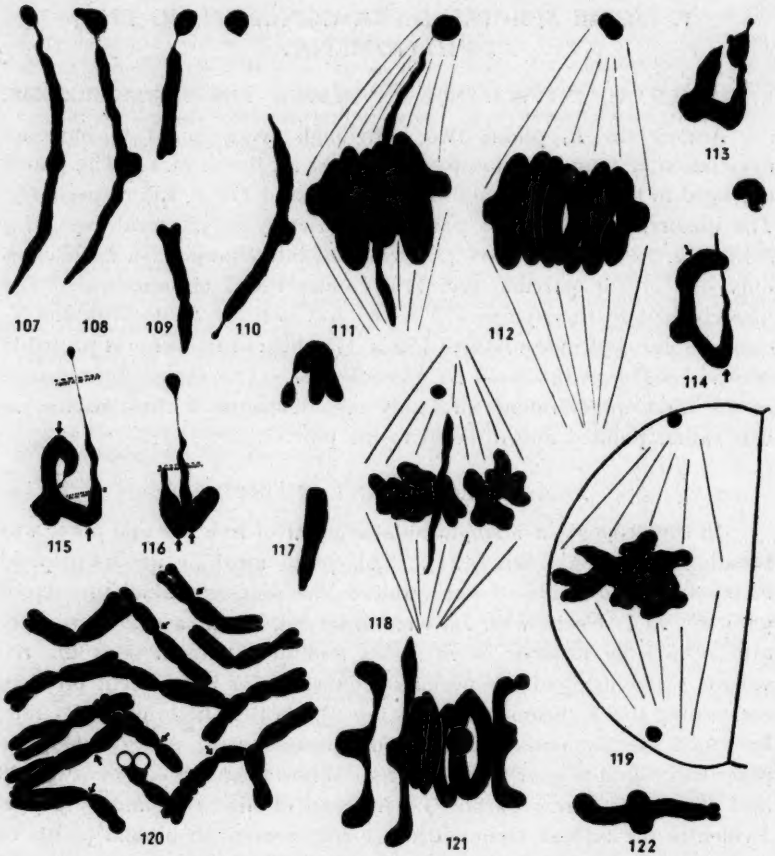
V. SOME SPECIAL DATA CONCERNING THE T-PHENOMENA.

1. SEGMENTAL INTERCHANGE INVOLVING THE T-CHROMOSOME.

Among the F_1 plants two individuals were found to have an association of four chromosomes in almost all the p. m. c. The plants belonged to the F_1 combinations 180 × 175 and 175 × 185 respectively. The quadrivalents in these plants were clearly of different type, this being due to different cases of segmental interchange. In both cases only one of the parents, line 175, carries the T-chromosome. The quadrivalent in the hybrid 175 × 185 has nothing to do with the T-chromosome, but in the hybrid 180 × 175 this chromosome is probably involved. This is indicated by Figs. 95—97. The upper chromosome in the three quadrivalents probably represents the T-chromosome, as it is rather pointed and directed to the pole.

2. A TRIPLOID PLANT IN LINE 129.

In the progeny of a single isolated plant of line 129 one plant was found to be triploid ($2n = 21$). This plant must be an autotriploid arisen from the union of one reduced and one occasional unreduced gamete. At I-M cells with 7_{III} were observed, but as a rule there were also a variable number of bivalents and univalents besides the trivalents. This triploid is especially interesting for the present problem concerning the T-chromosomes, as line 129 is the »high-intensity» line, in which the T-phenomena are most pronounced. As expected, the plant was found to have three T-chromosomes (Figs. 98—106). Figs. 98 and 99 show two separate T-trivalents of the ring-and-rod type. Evidently the typical asymmetrical T-ring present in diploid plants of line 129 is but little altered by the addition of a third chromosome. The triple chiasma joining all three chromosomes is situated in the long arm. Thus, the free end of the rod is the T-end and this has also a rather pointed appearance. In the Y-shaped trivalent represented by Fig. 100 only two of the chromosomes have visible T-ends, the third end being of ordinary appearance. In Figs. 101 and 102 the T-chromosomes form a chain trivalent. Two of the chromosomes lie straight and are axially stretched, just like an ordinary T-rod bivalent. The two adjacent T-ends, joining the middle and upper chromosome, evidently prevent the formation of ordinary V-shaped trivalents. At any rate, T-trivalents of the latter kind have not been observed. Fig. 103, finally, shows the three T-chromosomes in the shape of one bivalent



Figs. 107—119. Formation of a chromatin blob by the T-chromosome. Figs. 107—110, separate T-chromosome pairs with a terminal blob at I-M or commencing I-A. In Fig. 110 the blob has recently been detached. Figs. 111—112, complete I-M groups. In Fig. 111 the chromatin blob is just separating from a T-rod bivalent. In Fig. 112 the T-ring bivalent is indistinguishable from the other rings; the blob at the pole was certainly detached from the T-ring at an earlier stage. Figs. 113—116, separate T-rings or similar bivalents forming a chromatin blob at I-M. The double dotted lines in Figs. 115—116 indicate the contours of the rest of the metaphase groups. Fig. 117, T-pair at I-A probably derived from a ring bivalent, the upper chromosome with a chromatin blob. Figs. 118—119, blob formation at II-M. Fig. 118, the blob just detached from the T-chromosome. Fig. 119, a small blob at each pole, the T-chromosome indistinguishable. (Figs. 107—117 are from 129 × 175 and reciprocally, Figs. 118—119 from 128 × 129.) Fig. 120, somatic metaphase plate in a plant of line 129. All chromosomes normal, with a median or submedian centromere. Six chromosomes with arms of clearly different length are indicated with arrows. Two of them represent the S.A.T.-chromosome pair, the other four in all

and one univalent. The former is of the typical asymmetrical kind met with in diploid plants (cf. Figs. 13—23), the latter has a T-end which is orientated towards the nearer pole.

At I-A two T-chromosomes pass to one pole, one T-chromosome to the other. Fig. 104 shows a complete I-A (somewhat intermediate between side and polar view) with two T-chromosomes and eight ordinary chromosomes in the upper group, one T- and ten ordinary chromosomes in the lower group. Figs. 105 and 106, finally, show separate T-chromosomes from other cells. The three T-chromosomes at I-A were as a rule quite easily distinguished from the other chromosomes.

3. DETACHMENT OF TERMINAL PORTIONS OF THE T-CHROMOSOME.

A quite peculiar chromosome behaviour, which may be important for the understanding of the T-phenomena, was observed in some F_1 plants and in one of the inbred lines (128). This was the formation and frequent detachment of big spherical chromatin bodies at the ends of the T-chromosomes, especially at I-M but also at II-M (Figs. 107—119). This phenomenon was especially frequent in two fixations of F_1 plants from 129×175 and 175×129. It was estimated that in these plants about 3 per cent of the I-M groups showed this deviating and rather striking behaviour. In other fixations of the same crosses the phenomenon was only occasionally seen. It was also observed in a few cases in material of line 128 and in an F_1 plant of the cross 128×129. A more detailed study may perhaps show that the phenomenon also occurs in still other categories of material.

Figs. 107—110 show some separate T-rod bivalents at I-M or commencing I-A (Fig. 109). In Figs. 107—109 a big chromatin blob is attached to the upper T-end, in Fig. 110 this blob has recently been detached. Sometimes the blobs are smaller, apparently not yet being fully developed and in still other cells the T-rod bivalents are of the usual type without blobs. The connection between the blob and the chromosome end may show all transitions between the relatively thick connection in Fig. 107 and the very thin one in Fig. 111. Fig. 111 shows a complete I-M in which the contrast between the ordinary chromo-

probability representing the T-pair and the pair showing a constriction at I-M in many lines (cf. Fig. 121). — Fig. 121, I-M group in a plant of line 128 »heterozygous» for the T-chromosome. The three rod bivalents represent (from the right): the S.A.T.-pair, the T-pair and the pair with a constriction (the B-pair of KATTERMANN). Fig. 122, rod bivalent, probably representing the S.A.T.-chromosome. One end with a visible (divided) satellite directed towards the pole. — × 3100.

somes and the T-bivalent is striking. *When the chromatin blob is completely separated from the T-chromosome it is always situated at the pole of the spindle or close to this point.* This is illustrated by Fig. 112, showing a complete I-M group. In this group there is no rod bivalent, only rings, and the particular T-ring cannot be distinguished. In this cell the chromatin blob must have been detached from one of the ring bivalents at an earlier stage. Several other cells showed exactly the same picture. That T-rings, and not only T-rods, may also form chromatin blobs is rather evident from Figs. 113—117. These »rings», it is true, are not closed (probably excepting Fig. 114), but, nevertheless, they represent another category than the straight rod bivalents (Figs. 107—111). In Fig. 113 the formation of the blob appears to occur at a subterminal section of the chromosome. Fig. 117 shows the T-chromosome pair at I-A. This pair has evidently been ring-shaped at I-M, like Figs. 113—114. A chromatin blob is visible at the upper chromosome.

Also at II-M detachment of chromatin blobs from the T-chromosomes seems to occur (Fig. 118). In the cell represented by Fig. 119 there are two such blobs situated at the poles. In all other cases there was only one blob.

The whole phenomenon needs a still more detailed study, but two facts are already quite clear, viz. the production of »chromatin» blobs from the T-chromosomes (generally *one* blob per cell) and the very marked tendency of these detached bodies to be situated at the poles. In a total of 23 cells (from one slide), the blobs were quite free from the T-chromosomes at I-M, and without exception they were situated at one of the poles (as in Fig. 112).

4. THE SOMATIC CHROMOSOMES IN LINE 129.

In order to study the T-chromosomes at mitosis root tips of the »high-intensity» line 129 were fixed. In 1941 three plants, raised from selfed seeds, were examined. All metaphase plates showed 14 chromosomes with median or submedian centromeres and without a trace of the T-phenomenon. A few anaphases could also be analysed completely. All 28 chromosomes appeared to be V-shaped, all 56 arms more or less clearly pointing to the equator and none to the pole. Thus, the T-phenomenon seems to be purely meiotic. Whether the T-chromosomes are visible at the gametophytic divisions, has not yet been possible to decide.

Fig. 120 represents a somatic plate of line 129. Six chromosomes

are indicated with arrows, viz. the real satellite-chromosome pair and the two pairs with the greatest difference in length between the long and short arms. These latter two pairs in all probability represent the T-chromosome pair and the chromosome pair with a constriction at I-M [indicated by KATTERMANN (1937, 1939) as B-chromosome]. The same three pairs are visible as rod bivalents in Fig. 121, representing a »heterozygous» T-plant from line 128. In all three pairs, chiasmata are to be found in the long arm only.

VI. DISCUSSION.

In 1939 KATTERMANN described the occurrence of a new karyotype in a rye variety selected from a highly inbred material. A total of 19 plants from ten different lines were examined, four of these plants being normal, six heterozygous and nine homozygous for a deviating type of chromosome. According to the author, this chromosome could only be distinguished at I-A and II-A. At these stages it differed strikingly from the other V-shaped chromosomes by being rod-shaped, one end leading the way to the pole. This terminal end was frequently found to carry small attached bodies, similar to satellites. The deviating chromosomes were called T-chromosomes. In the present paper we also speak of T-chromosomes, as the peculiar chromosomes observed in our material of inbred rye are evidently of essentially the same kind as those studied by KATTERMANN. This is quite evident from a comparison between the figures. Thus, of the three p. m. c. in Abb. 3 in KATTERMANN's paper, the upper one representing a I-M [1] obviously corresponds to Figs. 1—2 in the present paper. In the same way the cell to the right in KATTERMANN's Abb. 3 corresponds to Fig. 32 in this paper. Without going into further details, it may be stated that practically all the pictures of I-A and II-A drawn by KATTERMANN were recognized by us, and this is true of the »homozygous» as well as the »heterozygous» plants. Thus, there is no doubt about the homology of the phenomena. This is rather interesting, since the two categories of inbred rye were quite unrelated, being raised from different varieties. Whether even the same chromosome pair is involved, cannot be decided with certainty from the figures alone. Crosses between KATTERMANN's and our own T-lines should be made in order to settle this question.

As regards the interpretation of the observations, however, our

[1] KATTERMANN considers this to be an early I-A. Strangely enough he states that the T-chromosomes could not be distinguished at I-M.

conclusions differ from those of KATTERMANN. According to this author, the peculiarities of the T-chromosome are in all probability due to a terminal position of the centromere. The T-chromosome is supposed to have arisen by translocation from an ordinary chromosome with a submedian centromere. This chromosome is strongly suspected to be the S.A.T.-chromosome, since in somatic plates of plants with T-chromosomes at meiosis only two chromosomes with satellites were observed. After a theoretical consideration of the meiotic behaviour in plants heterozygous for the T-chromosome KATTERMANN also suggests that the T-chromosome may perhaps have two centromeres (or parts of centromeres), one terminal and one submedian.

Indeed, the striking behaviour of the T-chromosome, especially at first and second meiotic anaphase, strongly suggests the presence of a terminal centromere. However, the data gathered by us demonstrate that the normal submedian centromere is present and that there is no true terminal centromere in the T-chromosomes. Naturally, this view depends on the way in which the term centromere is defined.

According to DARLINGTON (1937, p. 573), a centromere is »a particle in the chromosome thread whose special cycles of repulsion and division determine the anaphase and terminalisation movements of the chromosomes». An essential property of the centromere is that from diplotene to second metaphase it holds the two sister chromatids of a chromosome together. With respect to this property Figs. 45—46 are of special importance. These figures represent pairs of interphase nuclei in F_1 hybrids »homozygous» for the T-chromosome. In these nuclei the T-chromosome can be distinguished with certainty from the other chromosomes. The point of junction of its chromatids, however, is not terminal or subterminal, but submedian, the difference in length between the two arms being rather pronounced. That the apparent terminal centromere does not keep the chromosomes together was also observed, though less strikingly, at I-A. In many of the Figs. 31—42 it can be seen or inferred that the chromatids are held together by a submedian centromere. The same thing is repeated by the somatic plates of line 129 (Fig. 120), only showing chromosomes with median or submedian centromeres. T-phenomena were not seen at all in the somatic divisions of line 129. Evidently, they only occur at meiosis. — From Figs. 45—46 it is also clear that the T- and the S.A.T.-chromosomes are not identical, not in our material at least.

It has been observed in many organisms that terminalisation of chiasmata is always away from the centromere. In part of the ring

bivalents in Figs. 13—23 the position of the submedian centromeres discussed above is indicated with arrows. The T-ends also are clearly visible in most of the rings. The chiasmata connecting the T-arms are terminal or subterminal, and hence they have probably moved away from the normal submedian centromere and not away from the apparent terminal centromere.

The mechanism of metaphase orientation and anaphase movement has been subject to much study, and many theories about the rôle of the poles and the centromeres and the forces of attraction and repulsion have been advanced. According to DARLINGTON (1939 b), the meiotic metaphase represents a system of balanced repulsions between the two centromeres and between poles and centromeres. At anaphase the chromosomes move apart a short distance under the centric repulsions. At the same time the change to anaphase is helped by a waning of the repulsion from the poles. The later anaphase movement is due to the stretching of the spindle.

In our material of inbred rye showing the T-phenomena, *forces of attraction* between the T-ends and the pole must be responsible for the peculiar pictures observed. At all four stages, I-M and I-A, II-M and II-A, these forces of attraction could be traced and were found to intensify, oppose or modify the action of the normal submedian centromere.

In the T-rods of I-M (and I-A) the submedian centromere and the terminal forces work in the same direction, resulting in the long, straight T-bivalents represented by Figs. 1—9. As is clear from other evidence to be discussed below, the characteristic shape of these T-rods is partly due to an attraction between the T-ends and the poles. — The more or less ring-shaped chromosome pairs in Figs. 25—28 have no chiasma in the T-arm and are situated somewhat outside the metaphase plate. Their T-ends are directed towards the nearer pole and evidently do not repel each other. — The influence of the T-end attraction on true rings is quite analogous with that on the open rings, as may be seen from a comparison of Figs. 12—23 with Figs. 25—26. The T-end attraction to one of the poles changes the symmetrical ring into the characteristically distorted T-ring. Further, it was observed that the closed T-rings — just as the open ones discussed above — were often lying partly outside the rest of the metaphase group (Fig. 12). In such cases the typical shape of the T-rings was on an average more pronounced than in cells having the T-rings in an equatorial position. This is probably due to the fact that a displaced T-ring will be influenced

especially strongly by the attraction between the T-ends and the nearer pole. It is even probable that the entire T-ring is actively displaced by this attraction. If the T-ends have an exactly equatorial position there will be an equilibrium, in the opposite case they will come under the special influence of one of the poles.

At late metaphase and I-A the two T-chromosomes separate, presumably owing to the repulsion between the submedian centromeres. Those T-ends which from the beginning were not directed towards the pole to which the chromosome moves evidently turn round and change direction. This turning-round can be concluded from part of the anaphases in Figs. 31—42.

The evidence of the normal function of the submedian centromere and of the attraction between poles and T-ends is still more convincing at the second division. At II-M (Figs. 47—51) the submedian centromere and the long chromatid arms are situated at the equator. The »short» arms, however, are stretched towards the pole. Just as at I-M the two T-ends in each cell are attracted either towards the same or to opposite poles.

Second anaphases derived from the first type of II-M are especially interesting. As is clearly evident from Fig. 52 and the cells to the left in Figs. 53—54, both T-ends are directed towards the same pole. However, during the anaphase movement, presumably started by the repulsion between the submedian centromeres, the »short» arm of one of the T-chromosomes is drawn out into a thin thread. The end of this thread is still strongly attracted towards one pole, while the centromere moves towards the other pole. Finally, the centromere succeeds in pulling the T-end over the equator out of the influence of the opposite pole. The next stage is evidently characterized by the fact that the T-end turns round, now coming under the influence of the pole to which the centromere is moving. This turning-round is rather clearly seen in one chromosome of Figs. 55 and 56.

From the preceding evidence it is clear that the T-end does not possess a true centromere and that its typical reaction consists in an attraction to the nearer pole. This conclusion was reached from an analysis of meiosis in the plants showing the T-phenomena most clearly pronounced. In order to gain a better insight into the real cause and nature of the peculiar T-phenomena, the evidence from the remaining material of lines and F_1 families must also be considered. The first thing then to be decided is the genetical character of the phenomena, i.e. to what extent they depend on structural differences, gene-control

or plasmatic influences. As regards the last-mentioned possibility, it can be stated at once that no evidence of plasmatic influences on the expression of the T-phenomena has been obtained. Thus, in most F_1 hybrids both reciprocal combinations were examined and found to behave in quite the same way.

The characteristic behaviour of the T-chromosome is not shown with the same strength in all lines. On the contrary, different intensities could be distinguished, these intensities being described as high, medium and low. Other lines showed possible traces and most lines were entirely normal. The causes of these different intensities may be either structural or genic. *A priori* the latter alternative seems to be the more probable one. That the differences between the lines with various intensities of the T-phenomena are at least partly gene-controlled, may, indeed, be concluded from the chromosome behaviour in hybrids between such lines. In such F_1 plants there are no heteromorphic T-bivalents, both ends of I-M rods or all four T-ends at later stages often being similar in appearance. The intensity of the T-phenomena is, on an average, intermediate between those of the parent lines.

In a certain line (171) more than one chromosome pair (in extreme cases as many as 6 of the 7 pairs) behaved in a similar way as the single clear-cut T-chromosome pair of a »low-intensity» line. Unfortunately, crosses with line 171 have not yet been made, either with T-lines or with normal lines. It is practically certain, however, that such a general deviating chromosome behaviour is gene-controlled. As yet, we do not know whether the genes that are probably responsible for this general T-tendency are the same as those which influence the intensity of the phenomena in the special T-chromosome pair occurring in the lines 129, 128, 175 and 143. In this respect it is important to note that in line 171, showing the general weak T-tendency, a special T-pair showing the deviating behaviour more clearly than the other chromosomes could not be distinguished with certainty. This indicates that the special T-chromosome in the four lines mentioned above deviates structurally from its homologue in the line with a general T-tendency and in the normal lines.

Strong evidence as to the occurrence of a structural difference between the T-chromosome and its homologue in normal lines was, as a matter of fact, obtained from studies of meiosis in F_1 hybrids between lines with and without a T-chromosome pair. At I-M in those hybrids there was quite a low proportion of apparently heteromorphic rod bivalents consisting of one more or less typical T-chromosome, the other

chromosome being quite normal (cf. Figs. 69—78). Especially the study of later stages gave rather convincing evidence that structural chromosome differences are really involved. Numerous cells in various F_1 plants were studied carefully, but no cases were found with more than *two* of the four chromatids in a T-pair showing the characteristic deviating behaviour (Figs. 82—93). Thus, it seems necessary to conclude that the chromosome pair in question is really composed of two kinds of structurally different chromatids.

KATTERMANN (1939) was able to distinguish between reductional and equational separation of the T-ends at I-A in plants heterozygous for the T-chromosome. In our material, as in KATTERMANN's, the latter type of separation (Figs. 85—88, 93) was by far the more frequent, though reductional separation also occurred (Figs. 82—83, 91—92). The equational separation must be assumed to be the result of crossing over in the short arm.

The heterozygous F_1 plants discussed above never showed more than two chromatid ends with the T-character, and therefore this T-character is supposed to be due to a structural change. The two T-ends, however, were less pronounced than in the homozygous T-parent involved. This was especially clear in the cross of the »high-intensity» line 129 with the normal line 185, but seemed to occur in the crosses with the »medium» line 175 and the »low-intensity» line 143 as well. These observations again indicate that the T-phenomena are highly gene-controlled. An additional interpretation, however, is also possible, at least theoretically. Only a decreased intensity of the T-phenomena (in the two T-chromatids) was observed, never an increased intensity. This suggests the possibility of a rather direct influence of the normal chromosome on the behaviour of the partner chromosome. The normal chromosome may tend to prevent the T-chromosome from showing its characteristic peculiarities. However, the data now available are not sufficient to allow definite conclusions in this respect.

Additional evidence of a special kind concerning the peculiar attraction between T-ends and poles was obtained from the hybrids 129 × 175 and reciprocally. At first metaphase and anaphase in the slides of these hybrids a big blob was rather often seen at the end of one of the T-chromosomes (cf. Figs. 107—117). Often this blob is detached (Figs. 110, 112 and 114), and in such cases it was always found to be situated at one of the poles or close to this point (Fig. 112). Similar pictures were also observed at II-M (Figs. 118—119). — The process underlying these pictures is not understood at present. More in-

formation may be obtained by trying new staining methods, e.g. the technique for differential staining of nucleoli and chromosomes devised by SEMMENS and BHADURI (1939). The first thing to decide is whether the blobs represent chromatin or nucleolar material or some other substance produced by the T-chromosomes. As the blobs are evidently vigorously attracted to the pole, this probably has something to do with the attraction between poles and T-ends in T-chromosomes not showing visible blobs.

Considering all data from lines and F_1 hybrids, it may be concluded that the attraction of the T-ends to the nearer pole in the lines 129, 128, 175 and 143 is conditioned by some special chromosome structure not present in the normal lines. At the same time the T-phenomena are certainly also gene-controlled. Finally, the possibility of a rather direct interaction between T-chromosomes and normal chromosomes should be kept in mind.

The conclusion that the inbred lines studied differ in chromosome structure is in good accordance with other data, special as well as general. Thus, it is now rather clear that structural chromosome differences frequently occur in allogamous populations (cf. MÜNTZING, 1938, 1939). Recent data demonstrating a degree of structural hybridity so far unknown among plants were obtained by DARLINGTON and LA COUR (1940, 1941) in *Trillium* and *Fritillaria*. This was done by means of cold treatment, which revealed the occurrence of heterochromatic segments of different size and position. The structural hybridity demonstrated was mainly confined to the heterochromatic regions but in some cases also involved the euchromatin. The same cold treatment method was also tried for rye by LEVAN (1942). He succeeded in differentiating 10 of 14 chromosomes, and concludes that the rye chromosomes have heterochromatic end-segments in their shorter arms. In this connection it should be observed that it is the short arm of the T-chromosome which shows the peculiar phenomena described in the present paper. In the line with a general T-tendency it also seems to be the shorter arms which are involved. This indicates some connection between the T-phenomena and the heterochromatin-cycle. — By further work with the cold treatment method it should be possible to get precise information about the occurrence of structural hybridity in rye populations and structural differences between the inbred lines. Studies of meiosis in population plants of two rye varieties have already revealed the occurrence of a certain degree of structural hybridity, including

cases of segmental interchange and inversions (MÜNTZING and PRAKKEN, 1941).

The postulated structural difference between the inbred lines showing the T-phenomena and the other, normal, lines may evidently go back to differences already existing in the population. It is also quite possible, however, that it has arisen during the course of inbreeding. As first demonstrated by LAMM (1936), the meiotic mechanism is frequently disturbed in inbred lines of rye. On an average the chiasma frequency is lower, and non-conjunction and other irregularities are characteristic of certain lines. From our own experience we are able to verify LAMM's results. During our work with inbred rye many different kinds of irregularities have been studied, which will be reported in a future publication.

It was concluded above that the T-phenomena are also controlled by the genotypical constitution. The occurrence of genotypical control of the chromosomes at mitosis and meiosis is well known from many other organisms. DARLINGTON (1937) has summarized a number of such cases (l. c., pp. 53—60 and 395—419), and it seems superfluous in the present connection to go into details about this literature. It should be observed, however, that in most cases this gene-control affects all the chromosomes (as seems to be the case in our line with a general T-tendency) and not only a special pair as in our lines with one T-chromosome pair.

It was shown above that the T-chromosomes have only one centromere of the ordinary kind, keeping the chromatids together, and that this centromere has a submedian position. At the same time it is clear, however, that the T-ends have peculiar properties, simulating the presence of a terminal centromere. This is quite interesting especially in the light of RIBBANDS's observations on prophase associations in Diptera (RIBBANDS, 1941). According to this author, association between the end and centromere regions of non-homologous chromosomes was a common occurrence and was especially clear in the species *Habropogon appendiculatus*. The main cause of these and similar associations is probably mutual attraction between ends and centromeres, and, in certain circumstances, centrosomes. It is pointed out that chromosome ends resemble centromeres in some properties.

RIBBANDS's results do not help us to explain, however, why a chromosome end may behave like a centromere in some cases and not in others. The problem might be further elucidated by a more perfect knowledge of the constitution of the centromere. Some new interesting

data have already been obtained by DARLINGTON (1939 a) from a study of the misdivision of the centromere in *Fritillaria*. The author finds that the centromere has a complex structure, consisting of fluid as well as fibrous elements. The latter may be composed of several centrogenes. SCHRADER (1936), studying the amphibian *Amphiuma tridactylum*, also found the centromere (= kinetochore) to be complex, being composed of a »commissural region» and a »spindle spherule». MCCLINTOCK (1932), finally, working with ring-shaped chromosomes in *Zea*, obtained evidence that the centromere (= insertion region) in one case had been divided into two functional parts. — All this evidence indicates that the end of the short arm of our T-chromosome may really be derived from a centromere. As already suggested by KATTERMANN (1939, p. 298), it might represent part of an ordinary centromere. In such a case it may be supposed to perform only part of the functions of a normal centromere. At present this is only a guess, of course, but it may be mentioned as a working hypothesis. — In this connection it should be remembered that those regions of the satellite chromosomes which are involved in the formation of the nucleolus also seem to be complex. This was demonstrated by MCCLINTOCK (1934) in studies on the formation of nucleoli in maize. By a reciprocal translocation the nucleolus-forming region had been broken into two parts, each of which was found to be capable of forming a nucleolus. One of these parts, however, was a more successful nucleolar-organizer than the other.

The peculiar forces of attraction demonstrated to be at work during meiosis in the inbred lines having T-chromosomes and in the F_1 hybrids between these lines may perhaps be a peculiarity restricted to the ends of the short arms of the T-chromosomes. In such a case our observations are not necessarily in conflict with the general view, supported by many facts, that metaphase represents a system of balanced repulsions, and that the start of the anaphase movement is due to a repulsion between the centromeres and not to an attraction between centromeres and poles. At any rate, further studies of the phenomena now described are necessary, e.g. concerning the relation between the T-phenomena in plants with one special T-chromosome and in plants with a general T-tendency, the character of the supposed structural change, and the nature and origin of the terminal blob. Such studies will perhaps give some information of value concerning chromosome structure and the mechanism of meiosis.

VII. SUMMARY.

1) In four inbred lines of rye one chromosome pair behaved at meiosis in a special way, simulating the presence of a terminal centromere. In one of the lines the somatic chromosomes were studied and found to be entirely normal. A close study of these so called T-chromosomes showed that the true centromere is submedian, but that the ends of the short arm are *attracted* to the poles during metaphase and anaphase.

2) The peculiar meiotic behaviour of the T-chromosomes is displayed with different intensities in different lines, the categories high, medium and low intensity being distinguished. Some other lines showed possible traces of the T-phenomena, but most lines were entirely normal. In one line weak T-phenomena were shown by a variable number of chromosome pairs.

3) The occurrence of T-chromosomes in F_1 hybrids between inbred lines was studied. In hybrids between parents representing different intensities of the T-phenomena a T-chromosome pair was always present, the intensity of its expression, on an average, being intermediate between that of the parents. All four chromatids behaved in the same way, no heteromorphic chromosome pairs being observed.

4) In hybrids between parents with and without T-chromosomes the T-phenomena were rather weakly pronounced. However, a close study revealed the presence of T-ends, but more than two T-chromatids were never observed.

5) From these and additional special data the conclusion is drawn that the T-phenomena result from an interaction between the genotypical constitution of the various lines and a structural difference separating the lines with and without a T-chromosome pair.

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THE PLASTID DEVELOPMENT IN VARIOUS TYPES OF CHLOROPHYLL MUTATIONS

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PREVIOUS INVESTIGATIONS.

IT is a well-known fact that the numerous genotypic changes giving rise to chlorophyll mutations correspond to a rather limited number of different phenotypes, most of these belonging either to the *albina*, *xantha*, *alboviridis*, *viridis* or the *tigrina* group (GUSTAFSSON, 1940). Certainly the *alboviridis* and *viridis* groups are very heterogeneous, but nevertheless they remain rather well-defined from one another. Surprisingly few investigations have been devoted to the anatomical properties of the chlorophyll mutations, the papers of MILES, RANDOLPH, ZIRKLE and EYSTER having reference to mutations in maize, those of EULER and BERGMAN as well as EULER *et al.* to barley material. In addition, however, a great many papers have dealt with the features of the plasmatic or plastid changes which are non-mendelian in inheritance (cf. SCHÜRHOFF, 1924; KÜSTER, 1937; CORRENS, 1937; and MICHAELIS, 1940).

MILES (1915) expressed the view that plastids were altogether absent in *albina* of *Zea mays*, an opinion rejected and actually disproved by RANDOLPH in 1922. This latter author found that all chlorophyll types examined in corn (the normal strain, one *albina*, one virescent, and one maternal inheritance strain) showed the same initial cell structure, minute proplastids of identical size and appearance. The unusual characters of the mutant types were due to the failure of the proplastids to develop into plastids of the normal size, or colour, or both. Some of RANDOLPH's results were criticized by VON LOUI (1931). Nevertheless RANDOLPH was the first to show the important fact that *albina* mutations also contain plastids, although the plastid development is permanently retarded.

ZIRKLE (1929, cf. also 1926 and 1927) concluded that in all aberrant types studied by him in corn (*albina*, green-yellow, *aurea*, *argentea*, expallescent-virescent, and a maternal inheritance deficiency) the plastid primordia were normal, the divergent phenotypes being

the results of a delayed plastid development, a stoppage of development, or, finally, a stoppage of development followed by degeneration.

EYSTER (1929) made the discovery that no definite relationship seemed to exist in corn between the size of plastids and the development of chloroplastid pigments, in contrast to the state of things indicated by previous studies. *Albina* strains of maize could, in fact, be found with giant plastids. Therefore albinism could not be due to the failure of plastids to reach an optimum size, necessary for the development of chloroplast pigments.

EULER and BERGMAN (1933), as well as EULER *et al.* (1936), studied the plastid development in various spontaneous and induced barley mutations detected by NILSSON-EHLE and HALLQVIST. Of spontaneous types they studied *albina* 1, 2, 3 and 7 (the last-mentioned one not being a true *albina* but an *alboviridis* mutation), *xantha* 1, 2 and 3 and *alboxantha* (this type belonging to the *alboviridis* group in the wide sense of the word). Of induced types one *albina* mutation, one *xantha* mutation (Primus II »gulvit»), one *alboviridis* mutation (*xanthalba*) and two *viridis* mutations (Primus II *xanthaurea* and »gelbgrün») were examined. Unfortunately the methods used (fixed material) were not supplemented by sections on living material. The authors found that the shape and size of plastids were extremely irregular in the *albina* mutations: round, triangular, large and small, degenerating bodies occurring side by side. This result is presumably not correct.

None the less their studies strongly indicate (1) that the plastids of different *albina* mutations behave more or less similarly, (2) that those of *xantha* mutations are much larger and more regular than in the previous group, (3) that the plastids of *viridis* types differ rather inconspicuously from those of the normal material, and (4) that certain mutation types (as, for instance, *alboxantha*) have larger plastids than the mother strains. Apparently a certain parallelism exists between the phenotypical expression and the plastid development.

MATERIAL.

The writer's first study on these problems was undertaken in collaboration with Dr. O. GELIN, Landskrona, and dealt with various X-ray mutations in barley, fixed and treated in the same manner as indicated by EULER and BERGMAN in their paper from 1933. It was soon found that *viridis* mutations contained rather well-developed, almost normal chloroplasts but that the plastid size was somewhat variable, often smaller than in the mother line (Golden barley). In

albina mutations the fixative usually acted very badly, making the plastids alter their natural shape and size and giving them the irregular shape found by EULER and BERGMAN. As early as in 1940 it was concluded that this deranged appearance was presumably due to artefacts, only rarely to an actual degeneration. In most cases the plastids were rather minute. In favourable material they were found to be regular, round or oval bodies.

To solve the problem fully a series of mutations induced in Maja barley by treatment with 20,000 r-units were sectioned by hand in the autumn of 1941 and immediately studied under the microscope. Altogether 33 different cases of mutation were discovered in the X_2-offspring of 55 original X_1-plants, namely 10 *albinas*, 4 *xanthas*, 7 *alboviridis*, 11 *viridis*, and 1 *tigrina*. Successfully investigated were 5 *albinas*, 3 *xanthas*, 6 *alboviridis*, 4 *viridis*, and 1 *tigrina* type.

It must here be added that seeds of all cereals respond to such a heavy dosage as 20,000 r with an immense amount of chromosome disturbances (FRÖIER, GELIN and GUSTAFSSON, 1941). Most of these disappear during the ontogenesis, but many of them still reach meiosis. As a consequence, the mutations obtained result from an interplay of chromosome rearrangements, deficiencies and gene alterations. Presumably the results as to plastid development are in no way interfered with by the intense chromosome disturbances. In all instances leaves of young seedlings were sectioned, approximately fourteen days having passed from the time of sowing, the length of the seedlings being about 10 cm.

RESULTS.

Albina mutations. — Phenotypically these have but one expression, the white leaves being long and narrow, and in laboratory experiments usually having a rolled surface. Dwarf types are occasionally formed, likewise mutations possessing an open, fairly broad surface. In withering and dying leaves a very faint yellow-white tinge may develop at the tip, indicating the production of a slight amount of carotinoids (GUSTAFSSON, 1940).

This phenotypical uniformity is reproduced in the plastid behaviour. No such size variation as detected by EYSTER in corn and by FRÖIER (unpubl.) in oats was found. Generally the plastids are round or oval (ameboid) in shape, their outlines being regular and even. In many types they lie close to the cell-walls. The diameter varies considerably in different mutations despite the general minuteness of the plastids, so that in one case it was more than twice that of the smallest

diameter occurring. Chloroplasts in normal leaves are on an average from four to five times as large in diameter. Usually the number of plastids is greatly reduced.

EULER and BERGMAN attach great importance to a special phenomenon of vacuolisation in the plastids. Unfortunately this phenomenon could not be studied in the hand-sectioned material, but there is no reason to doubt its occurrence, since it is a common feature in various types of plastid destruction (variegation; SCHÜRHOFF, p. 173).

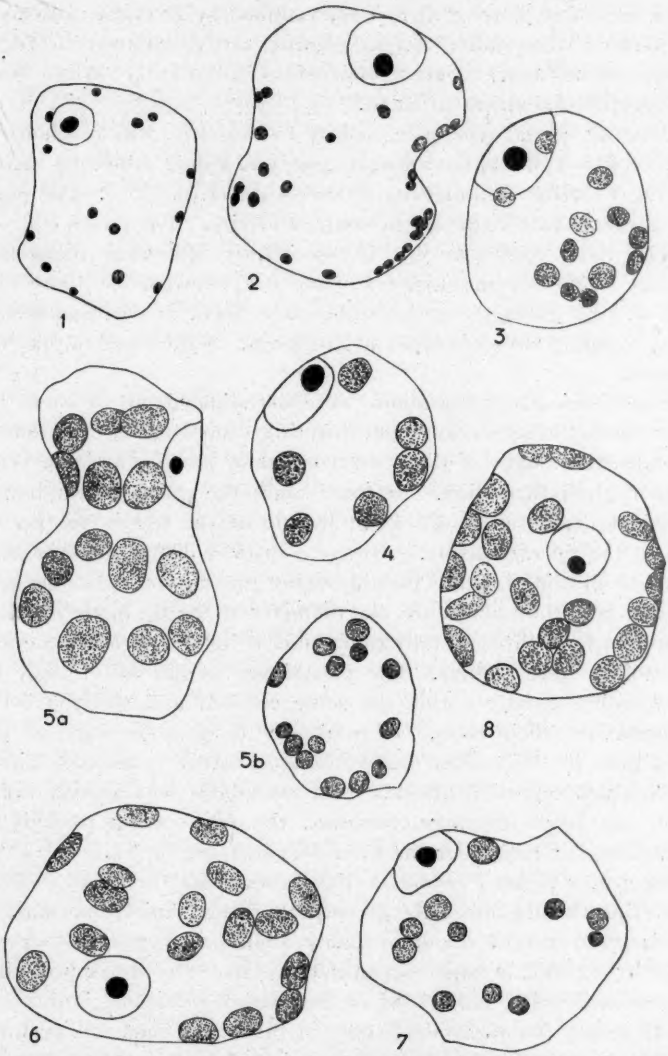
Xantha mutations. — In the writer's last three years' experiments the *xantha* group was classified according to definite phenotypic properties. The seedlings match yellow colours exactly, apparently without any gradation indicating chlorophyll, the colours being restricted to the numbers 151 to 250 (orange-yellow to yellow) in »Code des Couleurs» (KLINCKSIECK and VALETTE, Paris 1908).

Three mutations were examined, one having the colour 221, i. e. a rather weak-yellow gradation, one the colour 186, i. e. a conspicuous orange tinge, and one, finally, having the colour 171, i. e. a deep-orange yellow. All three *xanthas* contain larger plastids than were found in any of the *albinas* examined, the smallest plastids occurring in the lightest mutation. Here the plastids are also somewhat variable in size and shape. The largest plastids occur in the orange yellow type with the colour 186, where the plastids have a slightly smaller size than in normal leaves, their number per cell being about the same. In the other two cases the plastids are fewer in number.

In the spontaneous types *xantha* 1, 2 and 3 studied by EULER and BERGMAN the plastids were almost normal in size, showing however a rather pronounced irregularity as to shape, a property not detected in the hand-sectioned material. Vacuoles did not appear. The spontaneous mutations *do* contain some amount of chlorophyll, traceable even by the naked eye.

Summarizing we may say that the induced *xantha* mutations studied here possess better developed plastids than the *albina* mutations, although the plastid size, number and colour deviate from those of normal leaves.

Alboviridis mutations. — These are rather heterogeneous in appearance, but one feature in common is the differential development of colour at base and tip. A singular mutation type, arising infrequently in spontaneous and irradiated seed series, especially or exclusively after the irradiation of wet seeds, is the *alboxantha* mutation. Here the base of the leaf is bright-yellowish, the tip white or faintly yellow-white.



Figs. 1—7. Plastid structure in six different chlorophyll mutations in barley. — 1—2. *Albina* mutations (1941: 331: 128 and 152). — 3. *Xantha* mutation (331: 85, »Code des Couleurs» 221). — 4. *Xantha* mutation (331: 24, »Code des Couleurs» 171). — 5. *Viridoalbina* mutation (331: 333), tip (*a*) and base (*b*). — 6—7. Two different plants from a homozygous *tigrina*-like mutation (331: 216 and 218). In 6 a subnormal plant, in 7 a *tigrina*-like plant. — 8. Normal Maja barley from the same segregating progeny as the *viridoalbina* mutation.

Such a mutation (base or tip?) was examined by EULER and BERGMAN. The plastids were rather few in number, but to compensate for this they sometimes reached giant dimensions (compare EYSTER's finding with regard to albinism in corn).

Another special type examined by EULER *et al.* was *xanthalba*, the leaves of which should have a white base and a long yellow tip [actually they regarded this mutation as yellowish-green (p. 127)]. The plastids were rather small, irregular in shape and size.

The most common type of *alboviridis* mutations includes the frequent *viridoalbinas*, having a white or yellowish leaf base and a short or long green tip. These mutations seem to correspond rather closely to many virescent types in *Zea mays*. Some of them may reach maturity.

Five *viridoalbina* mutations were investigated, all of them being rather similar in appearance but differing somewhat in the gradations of colour, the length of the coloured part of the tip, and the velocity of chlorophyll formation. In three cases the plastid formation was studied at the base as well as at the tip of the leaves, in two more cases at the tip exclusively. Always a distinct difference existed with regard to plastid size, the plastids being much smaller at the faintly coloured base than at the tip, the diameter at the tip being in extreme variants at least three or four times that at the base. Most commonly the outlines were regular. The plastid size at the tip of some types varied rather greatly within the same cell but also differed between the mutations themselves. In one case the plastids were no doubt larger than in the normal leaves, looking rather giant-like (Figs. 5 *a* and 8, which represent plastids from two plants of a segregating progeny). In most instances, however, the *viridoalbina* plastids were slightly smaller and paler than the normal ones.

In a very peculiar mutation, the leaves being short and thick with brown tips, the plastids of the green parts looked entirely normal. Here the disappearance of colour probably implies a process of necrosis as found by FRÖIER in some oat mutations, the fully developed plastids already undergoing some kind of destruction in the beginning of the growth stage. No anatomical study of the brown part was performed.

The phenotypically heterogeneous but distinct group of *alboviridis* (*viridoalbina*) appears, consequently, to display a special feature of chloroplast formation, the rate of development being much higher at the tip of the leaf than at the base. Whether this parallelism would hold true universally, cannot be concluded so far.

Viridis mutations. — The *viridis* group is very heterogeneous, especially with regard to the intensity of the green colour. In this as well as in the writer's previous studies all mutations having a phenotypically detectable amount of chlorophyll distributed uniformly all over the leaf were ranked as *viridis*, beginning in »Code des Couleurs» with the number 251 and continuing to 303—307, which are the numbers of Maja barley. Many *viridis* mutations reach maturity and produce fully fertile ears. One *viridis* mutation was included in the yield experiments carried out in 1940 and 1941 (GUSTAFSSON, 1941 a and b). Frequently *viridis* mutations die in direct sunlight but mature in diffuse (ÅKERMAN, 1922; ÅKERMAN and FRÖIER, 1942). Subgroups of phenotypical interest comprise *virescens*, *chlorina*, *lutescens* and *albescens* types.

The *viridis* mutations examined by EULER *et al.* showed rather well-developed and normal-looking plastids. In the present study four different mutations were included, one of them being viable in homozygous condition and matching the colour 261, i. e. being yellowish—yellowish green (jaune vert). Two other types matched the colours 261 (yellowish green) and 276 (dark-green, but not blue-green as in the mother strain). The remaining mutation was described as a light *viridis*, but no exact measurement was made. The viable mutation contained well-developed, almost equal-sized, numerous plastids, somewhat smaller than those of the normal leaves. The dark-green mutation showed a similar plastid appearance, as was also the case in the non-viable type matching the colour 261. In the fourth instance a noticeable size variation was present, and the plastids were on an average smaller, approaching the appearance of a *xantha* mutation recorded previously.

No doubt the four *viridis* mutations — the viable as well as the non-viable ones — display an almost normal, a »subnormal», plastid development. This was shown to be the case also in the fixed material from 1940.

Tigrina mutations. — This peculiar mutation type is characterized by a repeated transverse destruction of the chlorophyll formation. The leaves are usually green with narrow constricted transverse regions, which are brown or yellowish. In laboratory cultures the leaf surface is rolled, not open as in *xantha* and *viridis*, and the tip is usually pointed. Extremely developed the *tigrina* cannot reach maturity. One *tigrina*-like mutation, showing a less pronounced transverse destruction, appeared in the X_2-progenies of an X_1-plant. In this instance the mutation

was able to mature, consequently giving rise to offspring homozygous for the recessive status.

Different plants from two homozygous recessive progenies were examined, one being almost green, the other one extremely *tigrina*-like. In the two progenies the plastids were strikingly different, in the subnormal one almost normal-sized although rather few in number, in the *subtigrina* considerably smaller but variable in size. In the latter case the plastids were certainly round in shape but with rough outlines and appeared to cluster together and finally to degenerate. If this interpretation is right, we notice here an example of a highly modifiable phenotype, partly viable, partly lethal. No doubt it will show itself to be excellent material for a profound study on the destruction of the chlorophyll apparatus. Unfortunately, no case of a true *tigrina* mutation has so far been examined in barley. Such a mutant in oats, however, has been subjected to analysis by FRÖIER (unpubl.).

The above-mentioned data indicate the occurrence of a parallelism between type of mutation and plastid development. *Albina* types usually contain very small, scarce plastids, *viridis* types subnormal ones. The *xanthas* occupy an intermediate position. In the case of *virido-albinas* the exterior appearance at the base and tip of the leaf directly reflects a different rate of plastid development. No general conclusions can be drawn, since the parallelism does not occur in maize and is less apparent in oats. It indicates, however, that many chlorophyll mutations in barley owe their origin rather to changes in the development of the initial plastid structures themselves than to the inhibition of chlorophyll and carotin formation exclusively.

The plastids have been assumed to constitute an independent hereditary organisation (plastom or plastidom), analogous to genome and plasmon. It is an important fact that none of the most extreme chlorophyll mutations, the *albinas*, lacks plastids entirely. As *albina* mutations generally die in seedling stage and consequently no homozygous offspring can be obtained, it is plausible that the minute plastids descend directly from bodies fundamentally normal and transmitted from the unfertilized egg-cell. Under the influence of the changed genomes (the recessive genes) they cannot later reach the functioning chloroplast size or state. This would be the same interpretation as was given by RENNER to explain the variegation in some *Oenothera* hybrids (1934). Here the plastom was normal. Together with special genomes it worked satisfactorily, together with some other genomes it was doing less

well, and variegation arose. [Cf. also CORRENS's ideas concerning the connection of the state of plasm and the non-mendelian type of variegation (1937)].

The question may arise: Can the chlorophyll apparatus be broken down so completely that plastids disappear altogether? We know that parasites and saprophytes, where photosynthesis does not occur, yet contain plastids, which are also able under certain circumstances to become green (SCHÜRHOFF, p. 166). Also in the case of variegation (Panaschierung) plastids are found in the albicate cells, although in old, purely white tissues they are frequently destroyed. These facts seem to indicate that plastid-lacking cells of higher plants do not exist except in combination with cells or tissues containing full-grown plastids or their predecessors. Possibly the developed or rudimentary plastids act upon some principal life processes, which are not necessarily connected with photosynthesis, and consequently cannot be entirely missing. In fact, such a plastid influence upon a quite different process (meiosis) was found and described by OEHLKERS in 1937.

A complete discussion of the anatomical data will be given in two further publications by the present writer and by FRÖIER (in preparation).

SUMMARY.

1. The plastid appearance was studied in five *albina*, three *xantha*, six *alboviridis*, four *viridis* and one *tigrina*-like mutation, induced in Maja barley by an X-ray irradiation with 20,000 r-units.

2. The plastids of *albina* mutations were usually minute, not actually degenerating, bodies having regular outlines. The plastid size varied in different cases.

3. The lightest *xantha* type had small, almost *albina*-like plastids, two other *xanthas* subnormal plastids.

4. The *alboviridis* mutations (*viridoalbina*) had a different rate of plastid development at the base and the tip of the leaf.

5. The *viridis* mutations contained almost normal plastids, or these were slightly smaller and paler than in the mother strain.

6. Two recessive progenies of a *tigrina*-like mutation were examined, one almost green, one extremely *tigrina*-like. The former showed subnormal plastids in the green parts, the latter type small, somewhat abnormal plastids. The phenotypic expression of this mutation varied considerably. Recessive plants may reach maturity.

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ABSTRACTS — KURZE MITTEILUNGEN

HARRY FEDERLEY: Chromosomenzahlen von vier Tagfaltern von ozeanischen Inseln.

Es ist eine bekannte Tatsache, dass Arten in verschiedenen Teilen ihres Verbreitungsgebietes verschiedene Chromosomenzahlen aufweisen können. Bei den Pflanzen handelt es sich in der Regel um Polyploidie. In den in klimatischer Hinsicht extremsten Regionen des Verbreitungsgebietes, wie in arktischen oder wüstenartigen Gegenden, wird die diploide Form nicht selten von einer polyploiden ersetzt. Auch bei Tieren kommt es vor, dass geographische Rassen durch verschiedene Chromosomenzahlen ausgezeichnet sind, und dass die eine diploid, die andere polyploid ist. Von solchen Tierrassen mit verschiedenen Chromosomenzahlen ist fast immer die eine bisexuell und diploid, die andere dagegen parthenogenetisch und polyploid. Ich erinnere an die bekannten Untersuchungen von ARTOM und seiner Schule an *Artemia salina* und von SEILER an *Solenobia.* Neulich hat E. SUOMALAINEN bei Coleopteren der Familie *Curculionidae* eine Serie mehrerer di-, tri- und tetraploider parthenogenetischer Arten gefunden, eine Entdeckung, die darauf hindeutet, dass Polyploidie bei parthenogenetisch sich fortpflanzenden Tieren vielleicht dennoch häufiger ist, als man bis jetzt angenommen hat.

Es gibt aber auch innerhalb einer Tierspezies geographische Rassen, die in bezug auf die Chromosomenzahl voneinander abweichen, wo der Unterschied jedoch nur ein oder ein paar Chromosomen beträgt. Hier ist dieser Unterschied vermutlich in einer Fusion oder einer Fragmentierung bestimmter Chromosomen zu suchen. Einen besonders schönen Fall hat SEILER nachgewiesen. Bei dem Schmetterling *Phragmatobia fuliginosa* hat es sich gezeigt, dass die Elbe die Grenze zwischen zwei Formen dieser Art bildet, von denen die eine 29, die andere 28 Chromosomen besitzt. FEDERLEY hat bei einigen Rhopaloceren-Arten festgestellt, dass die Chromosomenzahl bei den beiden Geschlechtern infolge von Fusion resp. Fragmentierung verschieden ist. Sowohl das Männchen wie das Weibchen kann ein Chromosom mehr als das entgegengesetzte Geschlecht haben. Er hat auch nachgewiesen, dass es Arten gibt, die in verschiedenen Gegenden von Europa oder sogar in verschiedenen Teilen Finnlands durch eine abweichende Chromosomenzahl ausgezeichnet sind.

Unter solchen Verhältnissen schien es mir von Interesse zu sein Material von gut isolierten Fundorten zu erhalten, wie z. B. ozeanische Inseln es sind. Man könnte sich denken, dass die dort heimischen Arten, die meistens als selbständige Rassen oder Varietäten beschrieben sind, auch im Chromosomenbestand Verschiedenheiten aufweisen würden.

Eine solche Gelegenheit geeignetes Material zu erhalten bot sich mir, als die Entomologen Dozent Dr. RICHARD FREY und Mag. phil. RAGNAR STORÅ im Sommer 1938 eine Reise nach dem Azorischen Archipel und Madeira unternahmen. Die genannten Herren hatten die Güte die Ovarien von vier Tagfalterarten zu fixieren und mir diese zur Verfügung zu stellen. Ich gebe hier die Beschreibung der Chromosomen der ersten Oozytenteilung.

Pieris brassicae azorensis RBL. Von dieser als endemisch betrachteten

Form (REBEL) habe ich die Ovarien von zwei auf den Inseln Sao Miguel, Ponta Delgada, und Fayal, Horta, gefangenen Faltern untersucht. Beide zeigten in mehreren Platten die Chromosomenzahl 15, also dieselbe Zahl, die die auf dem europäischen Kontinent und in England fliegenden Falter haben. In bezug auf Grössenverhältnisse der Chromosomen konnte ebensowenig ein Unterschied zwischen den azorischen und den kontinentalen Individuen entdeckt werden.

Colias edusa F. (*croceus* FOURC.). Die zwei von mir untersuchten Ovarien stammen aus Faltern, die auf Fayal, Horta, erbeutet waren. Beide enthalten zahlreiche Platten mit 31 Chromosomen, die von verschiedener Grösse sind, jedoch ohne ein besonders auffallend grosses solches, wie es *C. palaeno* hat.

Leider ist die Chromosomenzahl von *edusa* nicht bekannt, was um so mehr zu bedauern ist, da die Chromosomenverhältnisse in der Gattung *Colias* manches von Interesse bieten.

C. palaeno L. zeigt im männlichen Geschlecht die Chromosomenzahl 32 als die häufigste, nach zwei von mir untersuchten Männchen aus Pernå, Finnland, zu urteilen. Zwei Weibchen dieser Art, das eine in Pernå, das andere in Utsjoki an der 70. Breite gefangen, hatten dagegen beide 31 Chromosomen und unter diesen, wie gesagt, ein auffallend grosses (FEDERLEY).

C. hecla LEF. v. *sulitelma* AURIV., eine hochnordische Art, hat gleichfalls im weiblichen Geschlecht 31 Chromosomen (FEDERLEY).

C. nastes B. v. *Werdandi* ZETT., auch eine hochnordische Art, besitzt ebenfalls in den Oozyten 31 Chromosomen, die von verschiedener Grösse sind, jedoch ohne dass eines sich durch besondere Grösse auszeichnen würde (unveröffentlicht).

C. hyale L. Von dieser in Südfinnland seltenen Art ist es mir gelungen mehrere Exemplare zu erhalten: ein Weibchen aus Åland, ein Weibchen und zwei Männchen aus Esbo und ein Männchen aus der Nähe von Borgå. Alle drei Männchen zeigten in zusammen 25 Platten nur die Chromosomenzahl 31. Diese Zahl wurde auch in 6 Oozytenplatten des åländischen Weibchens festgestellt, wogegen das Weibchen aus Esbo in 5 Platten 32 Chromosomen aufwies. Unter den Chromosomen fällt keines durch eine besondere Grösse auf. Dagegen verdient vielleicht erwähnt zu werden, dass in allen 5 Platten des Esbo-Weibchens vier Chromosomen miteinander verbunden sind, während die 28 übrigen alle frei sind (unveröffentlicht).

Da die Chromosomenverhältnisse sowohl bei *C. palaeno* als *C. hyale* Verschiedenheiten in den beiden Geschlechtern zeigen, und da bei den beiden Weibchen der letzterwähnten Art ausserdem eine verschiedene Chromosomenzahl nachgewiesen wurde, die vielleicht geographisch bedingt ist, wäre es interessant die Chromosomenzahl von *edusa* in beiden Geschlechtern und aus verschiedenen Fluggebieten kennen zu lernen.

Pyrameis atalanta L. Ein aus Madeira, Funchal, stammendes Weibchen wies in zahlreichen Eiern die Chromosomenzahl 31 auf. Die Zahl, Form und Grösse der Chromosomen unterscheidet sich nicht von den bei finnländischen Exemplaren gefundenen (unveröffentlicht).

Lampides boeticus L. Das Material, ein Ovarium, stammt aus Fayal, Horta. 6 Platten mit exakt 24 Chromosomen wurden gefunden. Die Chromosomenzahl dieser in Südeuropa verbreiteten Art, die von FREY und STORÅ

zum ersten Mal auf den Azoren gesammelt wurde, ist unbekannt. Die Zahl 24 ist indessen eine bei den Lycaeniden häufig vorkommende. Unter den 17 von mir untersuchten Arten dieser Familie kam sie bei 9 vor.

Die gefundenen Chromosomenverhältnisse der insulären Exemplare zeigen also keine Abweichung von denjenigen der auf dem europäischen Kontinent fliegenden Falter, soweit sie bekannt sind (*Pieris brassicae* und *Pyrameis atalanta*), oder stimmen mit bekannten Zahlen nahe verwandter Arten gut überein (*Colias edusa* und *Lampides boeticus*). Die Isolierung scheint also bei den vier untersuchten Arten keine nachweisbaren Veränderungen der Chromosomenverhältnisse bewirkt oder befördert zu haben.

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ALBERT LEVAN and ÁSKELL LÖVE: Different chromosome numbers within the collective species *Carex polygama*.

The forms of *Carex polygama* SCHKUHR occurring in Fennoscandia are divided by modern taxonomists into three types: *C. Hartmani* A. CAJ., *C. Buxbaumii* WAHLENB. and *C. adelostoma* V. KRECZ. The three types are distinguished by a number of slight morphological differences, the most evident of which concern the shape and length of the spikes and the size and appearance of the floral parts.

They show differences, however, also in their geographical distribution. *C. Hartmani* has a decidedly southern distribution in Scandinavia, *C. Buxbaumii* has its main area in the pine-wood region of the middle and northern Sweden and in eastern Finland, and *C. adelostoma* is limited to the alpine mountain region and to the most northern parts of Scandinavia (cf. CAJANDER, 1935).

The three *polygama* types seem also to differ as to their ecology. *C. Hartmani* is a typical eutroph and needs a warm and continental climate, *C. Buxbaumii* is probably a eutroph too, even if its need of calcareous soil is not so absolute as that of the preceding form. It also requires a continental climate. Both *C. Hartmani* and *Buxbaumii* are rare in maritime regions; they are boreal but not arctic. *C. adelostoma* is probably a mesotroph. It needs only little lime and is less sensitive to the maritime climate. It may probably

be designated an arctic or boreo-arctic form. It goes as far down southwards as to Öland, where the isolated occurrence of other alpine species is also known, as for instance *Poa alpina*, *Bartschia alpina* and *Pinguicula alpina*.

The morphological differences present as well as the differences in geographical distribution between *C. Hartmani* and the other two *polygama* forms were considered significant enough by CAJANDER (l. c.) to justify the distinguishing of *C. Hartmani* as a species. The two northern types, on the other hand, were regarded by him only as varieties or subspecies. KRECZETOVICZ (1935) holds the opinion, however, that they also should be conceived as separate species.

Of the three forms, so far only *C. Buxbaumii* has been cytologically studied. HEILBORN (1924) gives the chromosome number at meiosis as $= \pm 37$ in material from Jämtland. It cannot be decided with certainty if the investigated plant belongs to the one or the other of the two northern species. But the assumption that the form in question is *C. Buxbaumii* s. str. is supported by the following observations: *1.* One individual in the neighbourhood of Abisko, Lappland, a dried specimen of which is shown to belong to *C. adelostoma*, has $2n = 106$, (LEVAN, in LÖVE and LÖVE, 1942). *2.* Pollen analysis of dried material has revealed that the pollen of *C. adelostoma* is somewhat larger than the pollen of *C. Buxbaumii*. *3.* The fruits of *C. adelostoma* are found to be 60—70 (average 64) units in length and 35—45 (average 39) in breadth, while the same measures in *C. Buxbaumii* are 52—60 (average 54) and 28—35 (average 30) respectively. Thus, besides the morphological, geographical and ecological differences previously mentioned as existing between *C. adelostoma* and *Buxbaumii* there is also present a cytological difference: *C. adelostoma* has a higher chromosome number than *C. Buxbaumii*.

The third species, *C. Hartmani*, the cytology of which is still unknown, has smaller pollen size than the other two species. Its fruit dimensions are 44—48 (average 47) units in length and 29—32 (average 30) in breadth. So presumably its chromosome number is lower than in *C. adelostoma* and *Buxbaumii*.

A closer study of the relations between the chromosome number, morphology, geographical distribution and ecology of the *C. polygama* species is planned.

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DORIS LÖVE: Intersexuality in *Melandrium rubrum* probably caused by a translocation between the sex chromosomes.

For a long time it has been known that among the strictly dioecious forms of *Melandrium rubrum* and *album* there also occur intersexual individuals in nature. These individuals can be divided into two groups, one genetically intersexual, the other phenotypically-physiologically intersexual. To the latter group belongs e. g. the apparent hermaphroditism of pistillate flowers when infected with *Ustilago violacea* (cf. CORRENS, 1928). It is not known as yet what kind of substance in the parasite causes the alteration in the sexual organs of the flowers, but it is possibly of a hormonic nature.

The genotypic hermaphroditism in *Melandrium* has been studied previously by, among others, SHULL (1911), HERTWIG and HERTWIG (1922) and WINGE (1931), who have all got similar results after selfing intersexual plants. SHULL and HERTWIG and HERTWIG assume that the intersexes are modified males in which a sex-determining gene has mutated. WINGE also supposes that the »hermaphrodites are males, whose X (in the given total gene combination) is strongly female in relation to the Y which is relatively weakly male» (p. 154).

The present writer has in her cultures of *M. rubrum* a number of intersexes, which all originate from the same locality in Scania (Konga, in the neighbourhood of Svalöf). These individuals are characterized by the occurrence of strictly male as well as hermaphroditic flowers on the same plant. The pollen grains appear to be rather fertile, and at least a certain degree of fertility (even self-fertility) is observed in the female organs.

The progeny after selfing these plants consists of females and intersexes and, so far, a single male. But as the parent plant also bears a number of strictly male flowers its morphologically male offspring may be counted among the hermaphrodite category.

Cytological investigations of the meiotic division showed that these intersexual individuals possess heterochromosomes, which, however, seem to differ from those which normally are seen in male individuals of this species. Some observations indicated that the size-differences between the two heterochromosomes were different from those of normal male plants. Therefore some attempts were made to measure the somatic chromosomes in the root-tip cells, fixed in LEWITSKY's 8 : 2 and stained with gentian-violet.

The sex chromosomes at mitosis of normal male individuals of *M. rubrum* are both clearly larger than the largest pair of autosomes. The X-chromosome has a distinct submedian centromere and is about 5,75 μ of length (the two arms being about 2,25 and 3,50 μ respectively). The Y-chromosome has a distinct median centromere and is about 7,5 μ (3,75 $\times$ 2) long.

The sex chromosomes of intersexual plants were very easy to distinguish, but it was also observed, even without measurements, that the »Y» differed from that of normal male individuals. Measurements showed that the smaller one of the heterochromosomes is a normal X-chromosome with submedian centromere, but the larger one, the »Y»-like chromosome, also had a submedian centromere. Its short arm was about 3,5 μ long, that is about the same length as the longest of the X-chromosome arms, and the largest arm

was 4,5—5 μ. *Therefore it may be assumed that the largest heterochromosome of my intersexual plants of M. rubrum is different from the Y-chromosome in normal male individuals.* The measurements also indicate that both these »heterochromosomes» might be *identical with normal X-chromosomes, the one of which, however, has got a piece, 2—3 μ long, translocated to its short arm.* The assumption that this piece is *derived from a normal Y-chromosome* is based primarily on the fact that the Y-chromosome contains very strong male-determining genes (cf. WESTERGAARD, 1940). If only a piece of the Y is translocated to a normal X there are great possibilities that the balance between the weakly female-determining X-chromosomes and the autosomes will be disturbed in such a way that the plant becomes intersexual and not fully male or female.

As most of the offspring after selfing the intersexes in 1940 and 1941 have not yet flowered, no information as to the distribution of sex can be given as yet. As mentioned above, the individuals which have already flowered are females and intersexes, but a single male also occurs. The theoretical distribution of sex, however, must be 1 normal female (XX), 2 intersexes (XX_Y) and 1 X_YX_Y-individual. That X_YX_Y-individuals should survive is to be doubted, but there still remain some possibilities, and then the individuals might be either intersexes or males.

It may be of some interest to note that individuals of just this kind have shown the greatest sensibility to sex hormones from the animal kingdom (LÖVE and LÖVE, 1940). After treatment with oestron on branches of the intersexual plants, sprouts with strictly female flowers developed. Strictly female flowers have not hitherto been observed on intersexual plants not treated with oestron. After treatments with testosteron strictly male flowers were also induced, but as such male branches also occur without any treatment, the action of testosteron may be somewhat doubtful in this case.

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ESKO SUOMALAINEN: Tetraploides Ei bei einer Aphide.

Vor einigen Jahren fixierte ich im Herbst nebenbei eine geringere Menge einer leider unbestimmt gebliebenen kleinen, glänzend hellgrünen Blattlausart, die an den Körbchenstielen und Blütenblättern von Treibhauschrysanthemen gefunden wurde. Die zytologisch untersuchten 5 Individuen waren parthenogenetische Weibchen. In den Ovarien sämtlicher liessen sich nur männliche Embryonen feststellen. Die diploide Chromosomenzahl des Männchens erwies sich bei dieser Art als 13.

In den Ovarien der Tiere waren, wie gewöhnlich bei den Aphiden, sich parthenogenetisch entwickelnde Eier in verschiedenen Entwicklungsstadien zu sehen. Insgesamt etwa zehn deutliche Metaphasen der Reifeteilung wurden gefunden. In sämtlichen erkennt man 13 Chromosomenelemente: 12 Dyaden (Autosomen) und eine aus zwei konjugierten X-Chromosomen gebildete Tetrade. Die Autosomen konjugieren also nicht in denjenigen Eizellen, die ♂♂ liefern, wohl aber die X-Chromosomen, wie bei den Aphiden auch schon früher festgestellt worden ist (SCHWARTZ, 1932, pp. 669—674; SUOMALAINEN, 1933, pp. 591—592). Analog damit sieht man in den Blastomerenmetaphasen der männlichen Eier 13 Chromosomen (Fig. 1), 6 kugelige und 7 langgestreckte. Eines der letzteren ist das X-Chromosom.

1 2

Fig. 1. Blastomerenmetaphase eines normalen diploiden Männcheneies. — Fig. 2. Blastomerenmetaphase des tetraploiden Eies. — CARNOY, HEIDENHAIN, 3000×.

In einem Ei, das sich im Stadium der Metaphase der 2. Furchungsteilung befand, zeigen beide Metaphaseplatten die Zahl von 26 Chromosomen (Fig. 2), also die tetraploide Zahl. Von den Chromosomen sind zwei augenscheinlich X-Chromosomen, die übrigen sind Autosomen. Beide Platten sind einander gleich. Zu bemerken ist noch, dass ihre Chromosomen deutlich kleiner als in den entsprechenden Kernen der diploiden Eier sind (vgl. die Figuren). Entsprechendes hat MORGAN (1915, p. 303) in den tetraploiden 1. Spermatozyten der Aphide *Phyllaphis coweni* festgestellt. Er fand im Hoden eines Männchens eine Zyste, deren sämtliche Zellen die tetraploide Chromosomenzahl aufwiesen. In diesen Zellen »the chromosomes are only half as large as are those at the corresponding stage of the normal spermatocyte stage, as seen in other cysts of the same testis». — Das in Frage stehende tetraploide Ei war sonst äusserlich in jeder Hinsicht normal.

Solche tetraploiden Eier sind bei den Aphiden sehr selten, denn das vorliegend besprochene ist vorläufig das einzige, das mir aus einer Fülle von zytologischen Präparaten mehrerer Aphidenarten begegnet ist. Die tetraploide Chromosomenzahl ist im fraglichen Ei wahrscheinlich durch Restitutionskernbildung entstanden. Es ist möglich, dass sich dieses Ei zu einem lebensfähigen tetraploiden Tier, in diesem Falle wohl einem Männchen, hätte entwickeln können. Im Falle eines entsprechenden weiblichen Eies könnte möglicherweise ein konstanter polyploider Aphidenstamm entstehen (vgl. SUOMALAINEN, 1940, pp. 122—125). Ein solcher würde, unter Berücksichtigung der vielen Besonderheiten im Entwicklungszyklus und der Zytologie der Aphiden, in

mancher Hinsicht ein besonderes Interesse darbieten. Ich habe darum vermittels Colchicinbehandlung einen polyploiden Aphidenstamm hervorzubringen versucht, vorläufig haben aber die Versuche nicht zu einem positiven Resultat geführt.

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G. NILSSON-LEISSNER: On the possibilities of breeding new, improved strains of timothy by means of selfing.

The experiments in question were planned and for the greater part carried out by Dr. NILS SYLVÉN during his time as head of the Herbage Plant Department of the Swedish Seed Association, Svalöf. A detailed report, now in the press, by Mr. G. JULÉN will appear in Sveriges Utsädesförenings Tidskrift 1942.

From a large material of timothy plants collected in different parts of Scandinavia and Germany extensive self-fertility investigations had enabled nine plants to be singled out as being specially self-fertile. The first inbreeding generation of these plants was sown in 1926 and studied for three consecutive years. The best plants of this I_1-generation were selfed and the I_2-progeny was sown in 1930. After repeated careful selections and selfings of the selected plants the I_3 was sown in 1934 and the I_4 in 1938. In 1930 clones of all mother-plants were planted for comparison side by side with their respective I_2-progenies, and in 1934 and 1938 all previous generations were grown as clones alongside their last inbreeding progenies. All the individual plants grown in these experiments were investigated for at least two years in respect of yield, regrowth, earliness, and rust resistance. The selection was in all generations very strict. Thus, out of 2432 I_3-plants only 199 were selected for production of the I_4-generation and these were all originated from 35 of the 377 I_1-plants of 1926.

In spite of the rigid selection the mean yield of the population as a whole decreased for each inbreeding generation. Correlations of yield between successive generations were computed in order to find out to what extent selection in one generation influences the yield of the next following one. Thus, e. g. in the trials of 1930, the I_1-clone plants were compared with the mean of their respective I_2-progenies. The following correlation coefficients were obtained: I_1—I_2: + 0,29, I_2—I_3: + 0,20, I_3—I_4: + 0,48. All were significant and the more so the later the generations. This proves that selection influences the yield of the next following generation and that this effect in-

TABLE 1. *Examples of strains having increased yield in later inbreeding generations. Mean yields of clones or strains (g) and relative figures (P = 100).*

Field Nos.	Year of planting	P		I_1		I_2		I_3-generation				I_4-generation			
								Selected plant		Whole strain		Selected plant		Whole strain	
		g	rel.	g	rel.	g	rel.	g	rel.	g	rel.	g	rel.	g	rel.
128—1—21—5.....	1934	370	100	300	81	330	89	810	218	302	82	—	—	—	—
	1938	390	100	290	74	270	69	650	167	—	—	950	244	473	122
Mean			100		78		79		193		82		244		122
132—8—21—8.....	1934	370	100	270	73	570	154	610	165	394	106	—	—	—	—
	1938	390	100	230	59	640	164	378	95	—	—	860	220	422	108
Mean			100		66		159		130		106		220		108
145—1—17—9.....	1934	370	100	270	73	520	141	560	151	348	94	—	—	—	—
	1938	390	100	610	156	680	174	470	120	—	—	1160	298	473	121
Mean			100		115		158		136		94		298		121
148—3—4—20.....	1934	370	100	240	65	380	103	520	140	340	93	—	—	—	—
	1938	390	100	260	67	320	85	720	185	—	—	960	246	467	119
Mean			100		66		94		163		93		246		119
368—11—22—13...	1934	240	100	280	116	420	175	450	187	247	103	—	—	—	—
	1938	420	100	310	93	200	47	333	79	—	—	950	226	551	131
Mean			100		105		111		133		103		226		131
550—7—6—2	1934	400	100	370	93	450	112	310	78	261	65	—	—	—	—
	1938	520	100	390	75	560	108	730	140	—	—	800	154	535	103
Mean			100		84		110		109		65		154		103
574—2—3—8	1934	400	100	400	100	300	75	410	102	284	71	—	—	—	—
	1938	520	100	530	102	640	123	570	110	—	—	1150	221	601	115
Mean			100		101		99		106		71		221		115

creases as the number of inbreeding generations increases. Generally a certain decrease of the mean yield from the P- to the I_1-generation could be ascertained. In spite of that, it has been possible to raise the yield of certain strains from generation to generation by means of selection. In some cases the mean of the I_4-strain was higher than that of the P-clone, and individual plants might yield twice as much as the latter. See Table 1. Thus, of the 199 I_4-lines, 27 gave a mean yield higher than their P-clones, and of the 2432 I_5-plants, 366 outyielded their P-clones.

The ability of regrowth formation was not generally influenced by inbreeding. Plants severely suffering from inbreeding depression, however, often had a very poor regrowth. On the other hand, self-vital strains, whose total yield had been raised during the inbreeding, generally had a better regrowth than their P-clones, both absolutely and proportionally. As a measure of earliness the time of incipient heading was used. Generally plants suffering from inbreeding depression were retarded in their development. The correlation coefficient of time of heading and yield of the I_4-generation was $-0{,}39 \pm 0{,}018$. In self-vital strains the most vigorous plants were somewhat earlier than the mean of the strain. Selection for earliness was very effective, as it could be shown that in this respect there existed a very strong correlation between successive generations. Between the I_3-clones and the corresponding I_4-strains the correlation coefficient was $+ 0{,}73$.

The most important disease of timothy in Sweden is rust (*Puccinia graminis phlei-pratensis*). In 1939, when the attack of rust was very severe, an increased susceptibility for this disease could be detected among the inbred plants. The difference in this respect was most obvious between the P- und I_1-generations, but was rather small and insignificant between the others. Certain strains were, however, very resistant throughout. Obviously, selection in respect to resistance is able to eliminate this increased susceptibility caused by inbreeding.

The investigation has shown that certain timothy strains are highly self-fertile and self-vital, giving rize to I_4-generations of higher yield than the original mother-plant. The same strains are also able to produce an abundant regrowth and develop early. Some of them are further highly rust-resistant. The possibilities seem to be good for the breeding of new, improved strains of timothy by means of selfing. The results prove the conclusions of CLARKE (1927) but contradict those of VALLE (1931) concerning timothy. Most probably these discrepancies are due to the different materials used in the individual investigations. The prospects for successful breeding by means of selfing seem to be better in this timothy material than those in rye reported by HERIBERT NILSSON (1937).

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STELLAN ERLANDSSON: Cytological studies in *Potentilla anserina* L. and closely allied Scandinavian species. (Preliminary note.)

In connection with taxonomic and phytogeographic investigations of *Potentilla anserina* L. and the closely allied species *P. Egedii* WORMSKJ. and *P. groenlandica* TRATT., I have also studied the chromosome numbers of these species.

The chromosome numbers have been calculated in root tips. These were fixed in NAVASHIN's fixative. The sections were cut 14 μ thick and stained with NEWTON's gentian violet.

The first notice about the chromosome numbers of *Potentilla anserina* was published by TISCHLER (1921—22). According to FORENBACHER, he gives the haploid number n = 16. Later it has been established that the basic number of *Potentilla* is 7, why the above-mentioned haploid number may be n = 14. New investigations of *P. anserina* give the somatic number 2n = 28 (POPOFF, 1935; TISCHLER, 1937; TURESSON, 1938). TISCHLER (1937) counts *P. anserina* to the polyploid species of the so-called Halligen-flora of the German coast of the North Sea. Finally, ROSCOE (1927) mentioned that a gigas-form of *P. anserina* has the haploid number about n = 22. Because of irregular divisions of the meiosis the correct number has not been established.

Potentilla anserina. — Material of this species I have received from about 50 localities from different parts of Europe, chiefly from Sweden. Most of the individuals have the somatic number $2n = 28$. Only in 8 cases another chromosome number has been found, viz. $2n = 42$. In some cases, the hexaploid biotypes have been found along with the tetraploid ones, e.g. Upsala, Arlöv and Dragør near Copenhagen.

Potentilla Egedii. — This species, which was at first described from Greenland, is found on the sea-shores of the Scandinavian coast of the Arctic Ocean and from the Gulf of Bothnia, where on the Finnish coast it reaches down into the archipelago of Pellinge in the Gulf of Finland.

From M. P. PORSILD, Mag. Sc., Disco, I have received Greenlandic individuals. These as well as the Scandinavian ones from 14 localities have the somatic number $2n = 28$. From Tromsø I have a biotype showing the hexaploid number $2n = 42$.

Potentilla groenlandica. — This species grows on the sea-shores together with *P. Egedii*. But its distribution is not sufficiently known. However, I have gathered 9 collections, and all have been cytologically investigated. Four collections are composed of biotypes with $2n = 28$ chromosomes, and three collections have biotypes with $2n = 42$. Finally, I have two collections with $2n = 35$ chromosomes. One of these is from Tromsø, and the other from Liinahamari on the Finnish coast of the Arctic Ocean. Both biotypes show bad fructification.

No differences in the size of the chromosomes were observed. The chromosomes of the three species are very uniform. They are of uniform thickness, bent, and of the same appearance as the chromosomes of the other investigated species. All the species are polyploid. It is noticeable that no diploid biotype has been found.

In a following paper I will give a complete list of the localities.

Botanical Institute, University of Stockholm, January 1942.

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ÁSKELL LÖVE: Physiological differences within a natural polyploid series.

Since the first polyploid form within a collective species was detected by PACE (1914) in the genus *Gyrostachys*, studies on the rôle of polyploidy in the evolution of plants have been undertaken by a great number of workers. As a rule the polyploids differ from their diploid relatives in some morphological characteristics, and almost always they show differences in their geographical distribution (cf. LÖVE and LÖVE, 1942). On the whole the polyploids are better fitted for inhabiting extreme climates than the diploids, a fact that has been postulated to be the result of differences in the physiological constitution of the different forms (cf. GYÖRFFY, 1941). Most of the studies on the physiology of diploids and polyploids have, however, been made on material consisting of experimentally produced autopolyploids, but not on polyploid series found in nature.

Some years ago the present writer began a close investigation on the polyploid series *Rumex* subg. *Acetosella*. This subgenus includes four dioecious species: *R. angiocarpus* MURB. ($2n = 14$), which is distributed in southern and south-west Europe, America and South-Africa; *R. tenuifolius* (WALLR.) LÖVE ($2n = 28$), distributed in the northern parts of Europe and Asia; *R. Acetosella* L. s. str. ($2n = 42$), with almost the same distribution as the tetraploid species; and *R. graminifolius* LAMB., a circumpolar, arctic species. All these species show quantitative as well as a few qualitative morphological differences (cf. LÖVE, 1941). As this material was suitable for certain physiological observations, some preliminary results obtained in the summer of 1941 may be reported.

Cell size. — The size of pollen grains increases proportionally with increase in chromosome number, as found in most other polyploid species previously studied. The volume of e. g. the stomata cells may be different in the diploid and polyploid species. However, a clear difference could not always be demonstrated between the three polyploid species, as also different ecotypes vary rather much in the size of the stomata cells.

Osmotic pressure. — The osmotic pressure in experimentally produced polyploids is mostly inferior to that in the diploid plants. In some cases, however, the osmotic pressure is somewhat higher in the polyploids, and in

all cases studied by GYÖRFFY (1941) the polyploids have greater possibilities to adapt their osmotic pressure to the climatic conditions.

Rumex subg. *Acetosella* showed, contrary to most of the polyploids previously studied, *a clear increase of the osmotic pressure correlated with an increase in chromosome number*. Plants in the same state of development were studied on several occasions during June and July, the osmotic pressure always being found to have increased somewhat in the direction $2x < 4x < 6x < 8x$. This fact may possibly demonstrate the causes of the differences in the geographical distribution of the four species of *R.* subg. *Acetosella*, as the high polyploid form without doubt inhabits more extreme climates than the diploid species.

Leaf pigments. — The diploid species *R. angiocarpus* has not so dark green leaves as the polyploid species. These differences were studied colorimetrically in an alcoholic extraction of the pigments of the same fresh weight of leaves. It was found that the diploid species possessed considerably less pigment than the tetraploid and hexaploid ones. Clear differences between the polyploid species could not, however, be demonstrated, perhaps because their variability is greater than is found in the diploid species. Some differences were observed between the pigment content of male and female individuals.

Oxalic acid. — All species of the genus *Rumex* possess some oxalic acid in their leaves and stems. An analysis of the three species *R. angiocarpus*, *R. tenuifolius* and *R. Acetosella* revealed that the diploid species gave the largest percentage of oxalic acid, the hexaploid form the lowest.

p_H of sap. — The p_H values measured in different leaves were found to be highest in the hexaploid species, lowest in the diploid one. The octoploid species was not investigated.

Ascorbic acid. — According to GYÖRFFY (1941) and others, the ascorbic acid content in diploid and polyploid forms does not bear a direct relation to the chromosome numbers. According to some other workers (cf. e. g. SANSOME and ZILVA, 1936), the ascorbic acid content may be almost twice as high in the tetraploid plants as in their diploid relatives. The results obtained from my studies on *R.* subg. *Acetosella* contradict all previously published data on the differences in ascorbic acid content of diploid and polyploid species, as *the vitamin C content decreases from the diploid to the tetraploid and to the hexaploid species.*

Photoperiodism. — The species of *R.* subg. *Acetosella* seem to differ in their photoperiodical reactions. The tetraploid and hexaploid species flower in the spring and high-summer, the diploid one, however, first in the autumn in my plots at Svalöf.

Summarizing the results obtained in the natural polyploid series *Rumex* subg. *Acetosella* it may be emphasized that in this series the cell size, the osmotic pressure, the pigment content, and the p_H of the sap *increase* proportionally to increase in chromosome number. The content of oxalic acid and ascorbic acid, however, *decreases* with increase in polyploidy. The diploid species may be a short-day plant, the polyploid species being long-day plants.

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